

**CHOICE OF SOCIAL ENVIRONMENT OF MALE BUFFALO
(*SYNCERUS CAFFER*) IN THE KRUGER NATIONAL PARK,
SOUTH AFRICA**

by

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DECLARATION BY CANDIDATE

I hereby declare that this dissertation submitted for the degree of MTech: Nature Conservation at the Tshwane University of Technology is my own original work and has not been previously submitted to any other institution of higher education. I further declare that all sources cited or quoted are indicated and acknowledged by means of a comprehensive list of references.

C.T. Hay

DEDICATION

This dissertation is dedicated to my wife and son.

*Kathleen, I am humbled by your unfailing love, encouragement,
and sacrifice which has made this work possible.*

I am eternally grateful.

*Dylan, may the wilderness of Africa bless you
with as much pleasure as it has afforded me.*

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I have been very fortunate to have the support and encouragement of a number of people during the conception, execution and completion of this work, and to whom I am greatly indebted.

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ABSTRACT

Sexual segregation has provided an enigma for researchers, and resulted in a number of hypotheses that attempt to explain this behaviour invoking behavioural, nutritional, environmental, reproductive and physiological-morphological arguments. The most promising of these hypotheses relate to two main concepts: optimising reproductive strategy (predation-risk hypothesis), and the effects of sex-related body size dimorphism (activity budget and forage-selection hypotheses). To assess the costs and benefits associated with different social environments I collected data on the movement, social affiliation, mortality, forage quality and testosterone levels of 166 known African buffalo from 2000 to 2006 in the Kruger National Park, South Africa. Adult males associating in male-only “bachelor” groups were 5 to 7 times more likely per unit time to be predated upon by lions than adult males or females associating in breeding herds. To counter-balance this cost, however, adult bachelor males generally ate higher quality food, moved ~30% less distance per day, and gained more body condition than did adult males in breeding herds. Changes in hormone levels and the timing of movements of bachelor bulls between social environments, allude to the fact that the bachelor phase is an important component of the breeding strategy of buffalo bulls. Recently, comparative analyses on a broad range of species suggest the activity-budget hypothesis as a common underlying cause of sexual segregation. Our intensive study, in an area with an intact predator community, however, strongly supported the predation-risk hypothesis as an explanation for sexual segregation in African buffalo.

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“I am going back to Africa soon. I don’t intend to shoot much. Certainly I will never kill another lion, nor do I intend to duplicate most of the trophies I have acquired on the last safari. But I will hunt Mbogo. In fear and trembling I will hunt Mbogo every time I see him, and I won’t shoot him unless he is a mile bigger than the ones I have got. I will hate myself while I crawl and shake and tremble and sweat, but I will hunt him. Once you got the buffalo fever, the rest of the stuff seems mighty small and awful tame.”-

Robert Ruark

CHAPTER 1

INTRODUCTION TO THE STUDY



African buffalo (*Syncerus caffer caffer*) have the distinction of being one of Africa's "Big Five" game species, and are an extremely valuable draw card for the growing eco-tourism industry in South Africa. Total game sales in South Africa for 2004 turned over in excess of R104 million (Damm, 2005a). In that year the hunting industry alone was estimated to have generated R890 million in foreign exchange, and in 2005 a buffalo trophy hunt could fetch up to \$18 750 (~ R122 000) (Damm, 2005b). No trip into the wilds is complete, whether tourist, photographer or hunter, without encountering buffalo, one of the stalwarts of the African experience.

Diseases such as brucellosis, theileriosis, foot and mouth disease (FMD) and bovine tuberculosis (bTB) can infect buffalo. Although often having minor or no ill effect on buffalo, these diseases may persist in infected populations and thereby act as disease reservoirs (Burridge, 1975; Vosloo *et al.*, 1996; Rodwell *et al.*, 2000). The potential for a spill over infection from buffalo to domestic livestock, and the associated economic consequences for agriculture have thus resulted in stringent control measures being placed on the movement of buffalo within South Africa. Buffalo populations in South Africa are classified into three regions according to their disease status, and in the Kruger National Park (KNP) they are infected with brucellosis, theileriosis, FMD and bTB. The presence of the latter in the population resulted in the initiation of a research project to determine the efficacy of various control strategies using mathematical modelling analyses of data collected longitudinally over a five-year period (Cross, 2005). Buffalo are a maintenance host of the disease in KNP (Keet *et al.*, 1996;

Rodwell, 2000) and an understanding of how the disease manifests in the population is thought to be fundamental to developing steps towards its management.

The only other reserve with a ‘diseased’ buffalo population in South Africa is the Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal, which is infected with theileriosis and bTB. The rest of the country’s populations are classed as ‘disease free’, most having originated from Addo Elephant National Park, in the Eastern Cape. There is thus a substantial demand for disease free buffalo, which fetch high prices at game auctions. In 2004, ‘disease free’ buffalo sold for an average of R148 867 (Damm, 2005a).

Burgeoning human populations and ever-diminishing natural habitats require prudent management of the region’s wildlife populations. This is vital to their conservation, and the growth and continued success of this industry. In this light, improved knowledge of the ecology of wildlife species, interfaced with wildlife management, is fundamental to achieving this goal.

The African buffalo is a member of the family Bovidae, tribe Bovini, which also includes cattle and bison (Skinner & Smithers, 1990). Historically buffalo were distributed widely in Africa south of the Sahara (Skinner & Smithers, 1990). Currently their distribution has become severely fragmented and they predominantly occur in significant numbers only in private and formal conservation areas (Winterbach, 1998). Buffalo are gregarious and can occur in large herds (hereafter referred to as breeding herds) sometimes numbering up to 3000 animals of all ages and both sexes (Skinner & Smithers, 1990). Herds aggregate and disperse depending on the season and local environmental conditions (Sinclair, 1977). Bulls may leave the herds to form all-male

‘bachelor’ groups over the dry season and rejoin over the breeding season, which coincides with the onset of the rains (Sinclair, 1977). The majority of calves are born between January and April in KNP (Pienaar, 1969), with other populations in Southern Africa following a similar pattern (Skinner & Smithers, 1990). Buffalo are classified as bulk feeders (Hofmann & Stewart, 1972), and require a plentiful supply of grass and water.

The ecology of the African buffalo has been the subject of number of comprehensive scientific studies (Grimsdell, 1969; Sinclair, 1977; Mloszewski, 1983; Prins, 1996). In southern Africa, studies have mainly been focused on the biology, ecology and behaviour of buffalo in breeding herds (Pienaar, 1969; Carmichael *et al.*, 1977; Conybeare, 1980; Funston *et al.*, 1994; Winterbach & Bothma, 1998). Elsewhere the behaviour and ecology of adult buffalo bulls has been investigated in two major studies in east Africa: Sinclair (1977) in the Serengeti, and Prins (1996) in Lake Manyara National Park, both in Tanzania. In Southern Africa two studies have focused on sexual segregation in buffalo, specifically relating to the behaviour of buffalo bulls. Turner *et al.* (2005) looked at time allocation of bulls in a buffalo population in HiP and Halley and Mari (2004) examined the seasonal social affiliation of buffalo bulls in the Chobe National Park, Botswana.

This study investigated the movement, mortality, forage selection, body condition and hormone status of buffalo bulls in a semi-arid environment in southern Africa. Buffalo bulls disperse from their natal herd once they are mature (Sinclair, 1977; Mloszewski, 1983), and regularly move between social environments (Prins, 1989b; Funston, 1992;

Halley & Mari, 2004; Turner *et al.*, 2005). They are therefore likely to be important agents for the spread of the disease within a buffalo population. An improved understanding of the behaviour of buffalo males would thus provide important insights into understanding bTB in KNP.

The results of this study lead to a clearer understanding of sexual segregation in buffalo and contribute to understanding the possible consequences of selective removal of males for hunting or culling purposes.

The objectives for this project were:

- To determine what movements buffalo bulls make between breeding herds and bachelor groups.
- To determine how these movements were related to the condition, size and age of bulls.
- To determine whether bachelor groups exploit better quality habitat than breeding herds.
- To determine whether bulls in bachelor groups hold an advantage in terms of condition gain and maintenance in comparison to bulls in breeding herds.
- To determine whether individuals associating in bachelor groups run a higher risk of predation than those associating in breeding herds.
- To determine whether testosterone is related to the movement of bulls between herd types.

Problem identification

Buffalo bulls are encountered in two social environments: herds ranging from 50 to over 1000 animals of both sexes, and smaller groups of bulls (Sinclair, 1977; Mloszewski, 1983; Prins, 1996). Sinclair (1977) called these bachelor groups 'bachelor' herds and described how old males associated in these groups year round, probably due to reduced fertility and reduced competitiveness with prime males. Prime and sub adult males tended to leave the herds during the dry season when there was no breeding taking place. Seasonal movements of bulls between herd types was also reported by Funston (1992) in the Sabi Sand Wildtuin, South Africa, who proposed that, due to their selection of riverine woodland habitats, bachelor males may be in better condition than herd bulls at the onset of the breeding season, giving them a competitive advantage in acquiring mates.

In Lake Manyara, Prins (1989b) found that, bull movement was related to condition gain in bachelor groups and condition loss in breeding herds, dominance relationships between bulls and breeding opportunities. Bulls were found to move regularly between social environments, and showed a low fidelity to groups in which they were seen. In contrast to temperate regions, however, Manyara buffalo showed no clear breeding season, and bulls could always expect to find some cows in oestrus (Prins, 1989b).

The tendency for males and females to live separately outside the breeding season is termed sexual segregation and occurs in many polygynous ungulates, especially north-temperate cervids and African bovids (Main *et al.*, 1996). Much attention has been

given to understanding sexual segregation in ungulates (Komers *et al.*, 1992; Komers *et al.*, 1993; Conradt, 1998; Conradt *et al.*, 1999; Ruckstuhl & Neuhaus, 2000). Ruckstuhl & Neuhaus (2002) reviewed the literature and identified the three most promising hypotheses:

1. Forage selection hypothesis
2. Activity budget hypothesis
3. Predation-risk hypothesis

The forage selection hypothesis predicts that females will use higher quality habitat than males, because of their less efficient digestive capability compared to males resulting from their smaller size. According to this hypothesis males would use habitat with lower quality but higher biomass food than would females. Gross *et al.* (1996), however, showed in the dimorphic Nubian ibex (*Capra ibex nubiana*) under controlled conditions, that both sexes digested their food equally well, and that females probably compensated for their lower digestive rate by masticating more thoroughly than males. If these results are broadly applicable to other species, it questions the validity of this hypothesis (see Main *et al.*, 1996; Ruckstuhl & Neuhaus, 2002).

The activity budget hypothesis also assumes differential digestive capabilities between males and females in dimorphic species and predicts that females, due to their lower digestive rate, will spend more time feeding and less time ruminating than males. It predicts that animals with similar activity budgets will form groups (Main *et al.*, 1996; Ruckstuhl, 1998; Ruckstuhl & Neuhaus, 2002).

Both of these hypotheses are reliant on sexual dimorphism and its assumed affect on the animal's digestive efficiency. In comparison to other dimorphic ungulates, buffalo show limited dimorphism: in the KNP the average mature male (660 kg) weighing c. 19% more than mature females (532 kg) (Pienaar, 1969) (compare: Kudu, *Tragelaphus strepsiceros* 51%; Bison, *Bison bison* 64.7%; Sitatunga, *Tragelaphus spekei* 89%; Nubian ibex, *Capra ibex* 111%) (Ruckstuhl & Neuhaus, 2002). In buffalo it is doubtful that this would lead to significant differences in activity, especially in semi-arid habitats where the strong seasonal fluctuations of the environment are likely to have an overriding effect on buffalo behaviour. In support of this, bachelor males in HiP spent similar proportions of time feeding per day as females (Turner *et al.*, 2005). However, mature bulls in the breeding herds spent less time feeding than females and bachelor males when oestrus females were present, and also showed higher faecal cortisol levels (Jolles, 2004; Turner *et al.*, 2005). It seemed therefore that social interactions between bulls competing for reproductive opportunities rather than differences in digestive capability were responsible for the different feeding times reported (Turner *et al.*, 2005).

The predation-risk hypothesis suggests that females and young, being more vulnerable to predation, will select areas that increase security to offspring, often with inferior but predictable sources of food quality and water. Males exploit areas of abundant, high quality food in all seasons in order to maximise size and strength for competitive interactions with other males during the breeding season (Main & Coblenz, 1996; Bleich *et al.*, 1997). Prins and Iason (1989) reported that adult buffalo bulls ran an almost three fold risk of being killed by lions (*Panthera leo*), compared to herd living

buffalo. In the KNP, Mills *et al.* (1995) reported the sex ratio of buffalo kills by lions to be 4.5 males per female before the 1992 drought.

In this study against the background of these hypotheses I attempt to clarify the function of sexual segregation in buffalo in southern Africa.

Description of the study area

This study was conducted in the central region of the KNP, South Africa between November 2000 and October 2004. The study was focused in the region of Satara rest camp (24° 23' S, 31° 46' E), predominantly on the ranger's sections of Satara, Kingfisherspruit, Nwanetzi and Tshokwane. In May 2003 additional animals were fitted with radio-collars on the Lower Sabie section (25° 07' S, 31° 55' E) in the southern region of KNP (Fig 1).

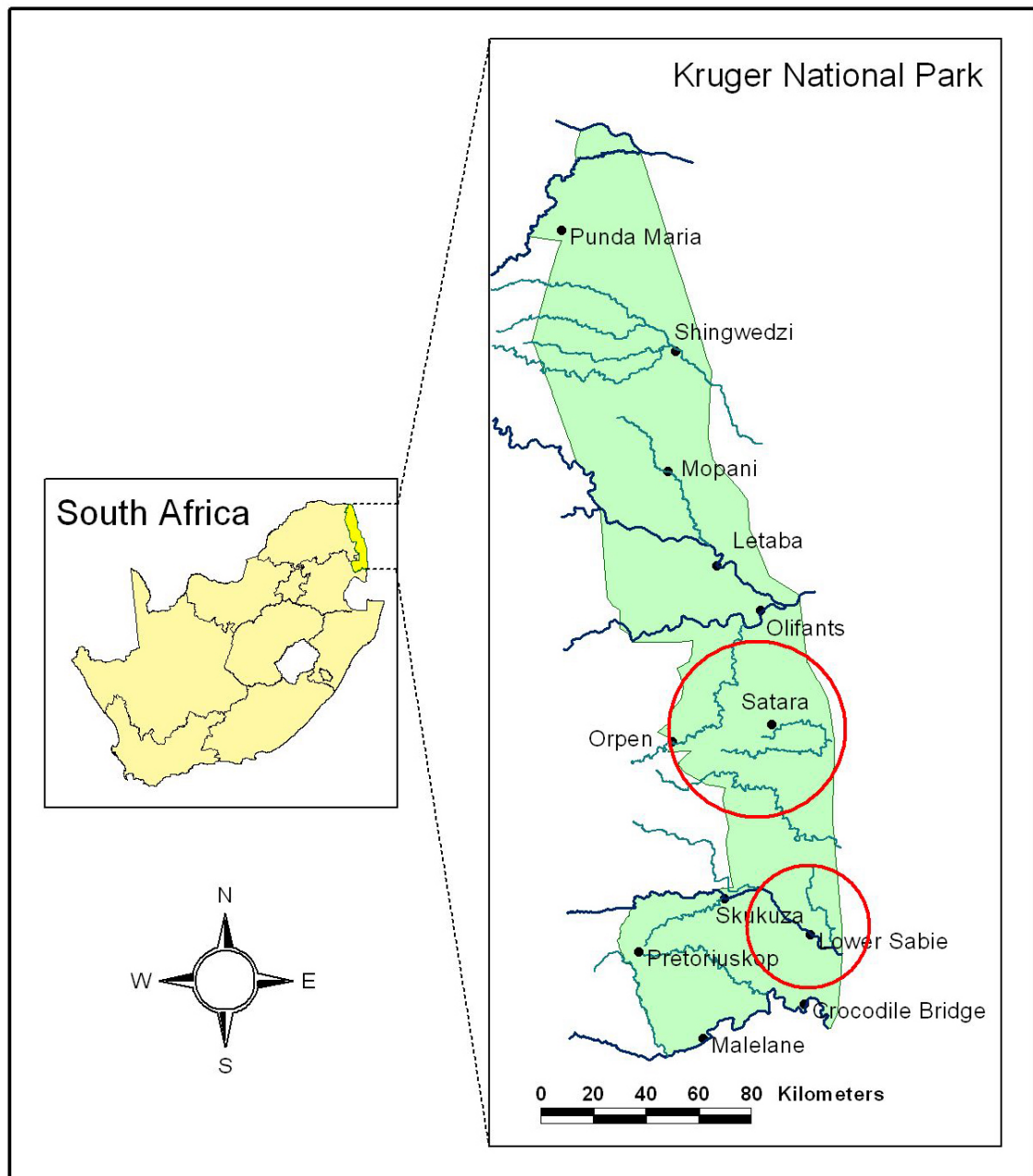


Figure 1. Map of the study area in the Kruger National Park.

The study area is characterized by acidic basalt formations in the east that consist of relatively flat plains with well-defined drainage channels. The Lebombo mountain range further east along the parks boundary is an undulating terrain with ridges and

bottomlands consisting of rhyolite and granophyre. The western half of the study area is a gently undulating landscape characterized by granite and gneiss substrata with intrusions of gabbro and dolerite. A strip of sedimentary Karoo sediments, predominantly eccla shales separates the basalt and granite formations along a north-south axis (Venter, 1990)(Fig 2).

Rainfall patterns in the KNP show a decreasing gradient from south to north (Fig 2), with a mean annual rainfall of 612mm at Lower Sabie and 548mm at Satara (Gertenbach, 1980).

The vegetation ranges from open to wooded tree and shrub savanna. The granitic landscapes in the west consist of moderate to dense bush savanna dominated by mixed *Combretum* spp., *Terminalia sericea* on the seepines and *Acacia* spp. in the bottomlands. Within this landscape, intrusions of gabbro result in a thorn savanna with dense grass cover which is often grazed intensively. These landscapes in the west commonly support kudu, giraffe, small groups of zebra, and wildebeest and impala in well grazed gabbro or sodic habitats. The east is dominated by open *Sclerocarya birrea* / *Acacia nigrescens* savanna, with a dense grass layer. Large numbers of wildebeest and zebra occur in this landscape resulting in a relatively higher abundance of large predators such as lion and hyaena. A thin strip of *Acacia welwitschii* thickets on karoo sediments separates the granite and basalts. This habitat forms dense thickets with palatable grass species that are often heavily grazed by a large numbers of zebra, wildebeest and impala, but also support browsers such as kudu and giraffe (Gertenbach, 1983).

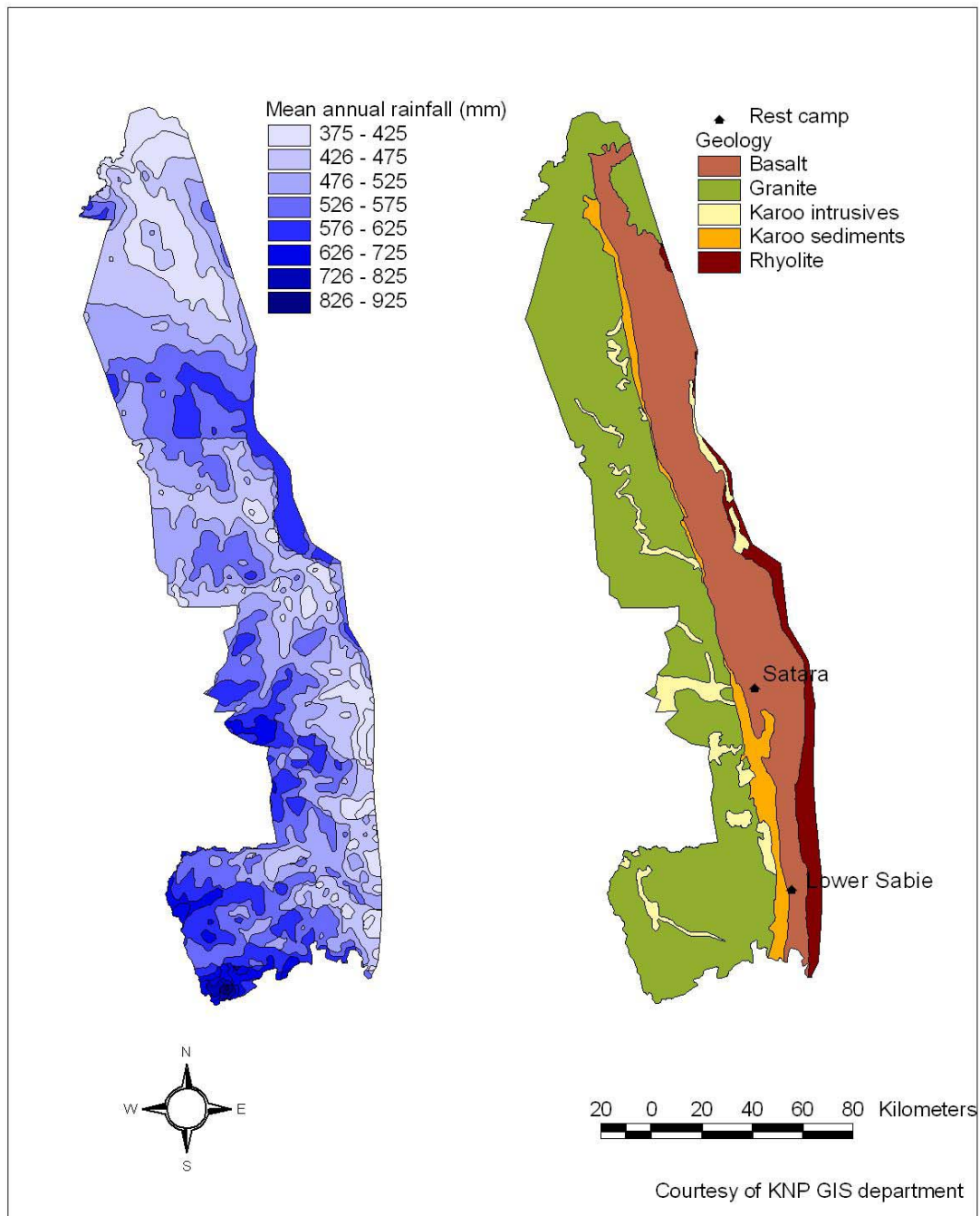


Figure 2. Maps of the geology and mean annual rainfall of the KNP.

Basic research procedures

This project was part of a larger research program that aimed to study the spread and impact of bTB in buffalo in the KNP. Over the study period we fitted VHF radio-collars (Telonics corp.) to a total of 157 animals of both sexes and various ages from one and a half years old. Buffalo use large home ranges in excess of 150 km², and due to the large number of collared animals we attempted to locate each radio-collared animal at least once a week. We restricted our fieldwork to daylight hours (summer 05:00 to 18:30; winter 06:30 to 17:30) due to restrictions on travel at night in the KNP. A large proportion of observations were conducted on foot due to large areas in the study area being inaccessible for vehicle access. When on foot, we minimized disturbance to the animals by remaining out of view, and through careful consideration of the wind direction.

We observed buffalo using Nikon Sporter I 10 x 36 binoculars and a Nikon spotting scope. After we located a herd its position was recorded using a Magellan GPS 315. We recorded data on a Palm Tungsten™ organizer using ThinkDB™ software. This enabled quick and easy transfer of the data onto a computer. The radio-collared animals that were present, the herd's general activity, and position in the landscape were recorded, and when possible the size of the herd, sex and age structure. Any known individuals that were visible were also recorded and body condition, current activity, approximate age and position in the herd were noted. When conditions were suitable we took video recordings of herds, such as when they crossed a road. We were able to obtain

additional data on the size of the herd, age and sex structure, known individuals present and body condition from video analysis.

Due to the ongoing bTB testing in the study area, a large number of buffalo had uniquely identifiable brands ($n = 562$). In addition to the radio-collared individuals a number of individuals ($n = 69$) were fitted with uniquely identifiable marker-collars in order to increase the sample size for re-testing of known animals for bTB. Certain buffalo also develop uniquely identifiable features, which may develop as they age. These features can include characteristic horns, facial markings, body scars and notches or cuts in the ears. This facilitated re-sightings of these known animals (males $n = 345$; females $n = 391$) opportunistically when they were encountered.

We aged animals according to criteria described by Pienaar (1969) and Funston (1992). In addition we spent time in the field with Dr C. Knechtel, to refine our aging technique. Dr Knechtel had spent the previous 8 years working on buffalo in the neighbouring Klaserie Private game reserve, and had certain known animals that she had kept track of since they were juveniles. She thus had a reasonably accurate estimate of the age of these animals.

Outline of the thesis

Chapter 2 describes the seasonal movement patterns of buffalo bulls in the context of age and social environment. I relate the mortality of buffalo to environmental measures

of predation risk, and for the first time, are able to show with empirical data the danger buffalo bulls encounter when associating in bachelor groups. In Chapter 3, I use measures of faecal nitrogen to estimate forage quality that buffalo bulls obtain in the two social arenas of the breeding herds and bachelor groups. I discuss differences in forage quality obtained in the two herd types, the daily movement of buffalo, and the implications for body condition gain leading up to the breeding season. In Chapter 4, I conduct an exploratory analysis on how testosterone is associated with buffalo movements between social environments and the physical characteristics of bulls. I discuss the insight this provides us to better understand the reproductive and social behaviour of buffalo bulls. Finally, in Chapter 5 I discuss the main hypotheses on sexual segregation in buffalo, summarise the results of this study and argue how it supports the most promising hypothesis. I also discuss how the results of this study apply to the management of buffalo and highlight areas for future research.

CHAPTER 2

BUFFALO MOVEMENT AND THE IMPLICATIONS FOR PREDATION RISK



Introduction

The tendency for males to segregate from females in sexually dimorphic, polygynous ungulate species is widespread, and has been the focus of a number of studies (Clutton-Brock *et al.*, 1987; Komers *et al.*, 1992; du Toit, 1995; Main & Coblentz, 1996; Bleich *et al.*, 1997; Ruckstuhl, 1998; Pérez-Barbería & Gordon, 1999; Mooring *et al.*, 2003). In Chapter 1, I reviewed the most promising hypotheses that have been proposed to explain this behaviour: (i) the predation-risk hypothesis, (ii) the forage selection hypothesis and (iii) the activity budget hypothesis (Main *et al.*, 1996; Gross, 1998; Main, 1998; Ruckstuhl & Neuhaus, 2002).

In buffalo, the seasonal switching of males between mixed-sex, breeding herd and male-only bachelor groups has been well described (Grimsdell, 1969; Pienaar, 1969; Sinclair, 1977; Mloszewski, 1983; Funston, 1992; Turner *et al.*, 2005). Mature bulls associate in the breeding herds during the mating season, and move into male only bachelor groups in the dry season, when breeding opportunities and food resources are limited.

Few studies, however, have specifically addressed sexual segregation in buffalo. Prins (Prins, 1989b) examined the social affiliation of bulls in Lake Manyara and attributed herd switching to temporal changes in body condition. More recently, Halley and Mari (2004), concluded that a combination of the activity budget hypothesis and predator avoidance best explained buffalo bulls social affiliation in Chobe National Park. In their study bulls spent the late dry season in the breeding herds, which differed from studies elsewhere in Africa. Further, Turner *et al.* (Turner *et al.*, 2005) studied activity patterns

of buffalo in HiP to determine if differences in time budgets or activity synchrony could explain segregation, and established that the activity budget hypothesis was not supported.

Numerous studies have shown reduced survival in adult males, and sex ratio's skewed in favour of adult females (Clutton-Brock *et al.*, 1982; Owen-Smith, 1993b; Berger & Gompper, 1999), including in buffalo (Pienaar, 1969; Prins & Iason, 1989; Funston, 1992). In polygynous species, males may adopt a risk-prone strategy (Clutton-Brock *et al.*, 1982; Hogg & Forbes, 1997), and reduced male survival is expected because of the demands of intrasexual competition (Owen-Smith, 1993a; Loison *et al.*, 1999), and the costs of large body size, especially in food-limited environments (Toïgo & Gaillard, 2003).

In this Chapter, based on this evidence of male biased mortality in buffalo, I investigate the seasonal movement and mortality of buffalo bulls in the KNP, where there is an abundance of large predators and highly seasonal environmental conditions.

This study has been one of the first to extensively use radio-collars on buffalo bulls (also see Halley & Mari, 2004), which are notoriously destructive to such equipment. This technology has for the first time facilitated reliable empirical data over a four-year period on the survival, movement and social affiliation of bulls, and provides significant insights into the ecology of the male buffalo.

Methods

We fitted radio-collars to a total of 72 male buffalo from the age of two years old. The majority of these animals were fitted with radio-collars during 2001 ($n = 40$), with additional individuals collared in subsequent years to maintain the sample size of bulls as individuals died: 2002 ($n = 14$), 2003 ($n = 7$), and 2004 ($n = 11$). Buffalo were darted from a helicopter and immobilized with a combination of M99 (etorphine hydrochloride) and Stresnil (azaperone). The age distribution of radio-collared animals and the length of time that the collars were fitted are shown in Table 1.

Table 1. The distribution of radio-collars fitted to buffalo bulls across four age classes over the study period (April 2001 – October 2004).

Age when collared	Total no. of individuals	Length of time collared (days)			
		Average	Min	Max	Total
1 - 2 years	16	509	2	925	8141
3 - 5 years	24	639	46	1299	15335
6 - 8 years	20	587	81	1299	11746
9 years plus	12	404	90	859	4852

Bull movement

The distribution of radio-collared animals was primarily around Satara camp in the central region of the KNP. Due to dispersal, however, marked animals were distributed at times as far north as Letaba camp (65km) and down to the Sabie River (83 km) in the south of the KNP (Fig. 1). We located radio-collared animals once a week from a

vehicle, using radio telemetry equipment between April 2001 and January 2006. In instances where we could not locate individuals for over a month we used an aircraft to locate them.

I classified buffalo herds into two groups: bachelor groups and breeding herds, the latter always contained a mix of bulls, cows, and immature animals. Bachelor groups contained bulls exclusively and ranged in size from one to 50 animals. Exceptionally, stray cows associated temporarily with bachelor groups. Once I had located the focal animal, I recorded the type of herd it was associating in, and any other focal animals that may have been present. It was possible to determine if an individual was present in a herd without visually locating it by using the radio-telemetry equipment. The fact that the herds were usually spaced many kilometres apart eliminated the possibility of confusion. Where possible I collected information on the number of animals in the group and the sex and age structure. For larger herds this was made possible by taking a video recording of the herd crossing a road or suitable open area, enabling a more accurate analysis later on.

Data on the movement of radio-collared bulls between herd types was analysed by calculating the proportion of time bulls were seen in breeding herds per month. I then grouped the data by season (breeding or non breeding) and age-category and averaged the proportion of time spent in the breeding herds. I accounted for the aging of individuals each year. This data was analysed using non-parametric statistics, as it was not normally distributed.

We recorded on an ad-lib basis, any direct courtship activities that we observed. This included mounting and actual mating. Our records of the amount of time we spent in the field over the study period showed that we spent similar amounts of time each month throughout the year observing buffalo (One-way ANOVA, $F_{(11,32)}=0.637$, $P = 0.784$). I was therefore confident that monthly variations in data were not skewed by an uneven distribution of the amount of time spent in the field.

I transformed the herd size data to the natural logarithm to stabilize the variances and used z-tests for the analysis.

Buffalo mortality

We collected data on the herd affiliation and mortality of buffalo on an ongoing basis between November 2000 and January 2006. The radio-collars contained a mortality alarm facility, which signalled when individuals were no longer alive, or had lost their radio-collar. A radio-collar that had fallen off an individual could be distinguished from a mortality event by the lack of any signs of a carcass, as well as the condition of the collar. I assumed that if the belting was broken and no carcass was present that the radio-collar had fallen off. This was confirmed in a number of instances when individuals were re-sighted later and established to still be alive.

Once we had located a radio-collar that was transmitting a mortality signal, we made an effort to locate the site where the animal had succumbed. The presence of rumen content and dried blood on the ground was indicative of such a site. If we could not pinpoint this location, we noted the location of the remains of the carcass. As far as

possible we tried to identify the cause of death, through inspection of the carcass and surrounding area for predator tracks, scats and other signs. The radio-collar itself almost always bore scratches, teeth marks and hairs caught in the rivets from predators during the process of killing and feeding off the animal. I concluded all predation events to be from lions, which is supported by the findings of two previous studies (Prins & Iason, 1989; Mills & Biggs, 1993).

I tested differential mortality of adult radio-collared males and females (5 years and older) in bachelor groups and breeding herds using a chi-square analysis. I estimated the expected frequencies from the number of radio-collar days that buffalo spent in each herd type. The fact that buffalo were not sighted every day resulted in gaps in the data between sightings where there was time in which I had to allocate herd type data to. I assumed that buffalo remained in a particular herd type if they were seen in the same herd type in the subsequent sighting. In cases where individuals switched between herd types, and a period of more than one day had elapsed before they were re-sighted in the new herd type, I allocated the time in two ways: (i) I allocated half of the time in-between the sightings to each herd type, and (ii) I allocated all the time to bachelor groups. The latter allocation of time is the most conservative in terms of estimating the largest expected frequency of mortality for bulls in bachelor groups.

We were not always able to determine in which herd type individuals were killed. As a result I conducted two analyses: (i) I only used mortalities where the herd type in which the individual was killed was known, and (ii) I used all mortalities and assumed the last herd type that they were sighted in to be the one in which they were killed. For the

former analysis (i), I also right-censored the radio-collar time of the individuals whose mortalities had been excluded. Adult mortalities due to reasons other than predation were excluded ($n = 9$), but the radio-collar time of these individuals was included in the analysis up to the point of their death. Exceptionally, radio-collared females spent time in bachelor groups (55 radio-collar days) or alone (71 radio-collar days). This time was excluded from the analysis as it resulted in expected frequencies of zero in the Chi-square analysis. This represented only 0.14% of the total radio-collar time (87 458 radio-collar days) and did not affect the outcome of the analysis.

I therefore conducted four separate analyses using the four criteria mentioned above. I also calculated the mortality rate of males and females in each herd type, by dividing the number of deaths by the total number of radio-collar days in each category.

I determined an index of predation-risk at each mortality site by using the maximum visibility at a height of 1.5 m. This approximates buffalo eye-level as adult buffalo measure between 1.3 and 1.5 meters at the shoulder (Pienaar, 1969). A field assistant walked away from the observer until he was no longer visible up to a height of 1.5 m (chest height). We measured the distance to the point at which he was last visible with a range finder. We repeated this measure for each of the four main cardinal compass directions, which I averaged to obtain an index of maximum visibility for each site. I normalised the data by using the natural logarithm of the average visibility. The data was analysed using a two-way ANOVA in STATISTICA (Statsoft, 1997) and tested at the 95% significance level ($P < 0.05$).

Results

Bull movement

The counts of bachelor groups over the study period indicated a seasonal change in average group size (Fig. 3).

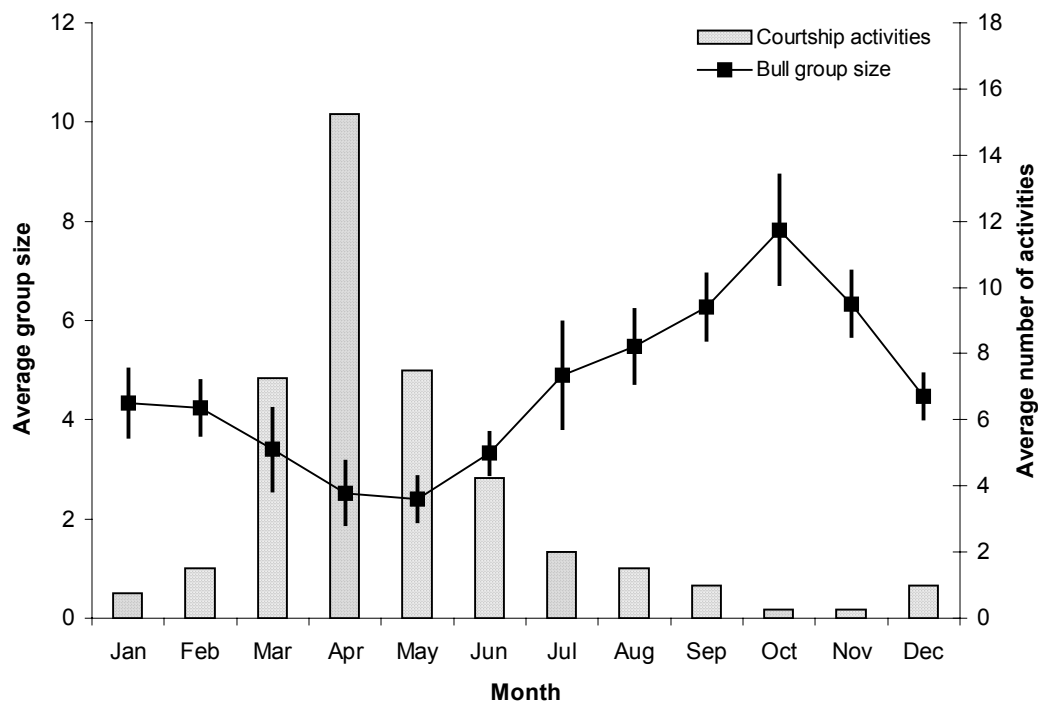


Figure 3. Average size of bull groups (line graph with solid squares) and average number of courtship activities observed (shaded bar graph) over the study period (2001 - 2004), grouped and averaged by month. Error bars indicate the standard error of the mean.

Average group size was largest towards the end of the dry season between September and November ($n = 191$, mean: 6.86, $z = 5.68$, $P < 0.001$, z -test), and declined with the onset of the wet season to reach a minimum between March and June ($n = 85$, mean: 3.04, $z = 5.68$, $P < 0.001$, z -test). The occurrence of courtship activities was greatest

between March and June, and reached a peak in April. There was a significant inverse relationship between courtship activities and bachelor group size (Spearman Rank Correlation Coefficient, $R_s = -0.851$, $n = 12$, $P < 0.01$). The peak period of courtship activity coincided with the time of year when average bull group size was at a minimum, and conversely, the period of least reproductive activity occurred at the time of year when bachelor groups were largest.

Data from the radio-collared individuals showed that bulls tend to spend less time associating in breeding herds with increasing age (Fig. 4) ($H = 469.76$, $df = 3$, $P < 0.001$, Kruskal-Wallis ANOVA).

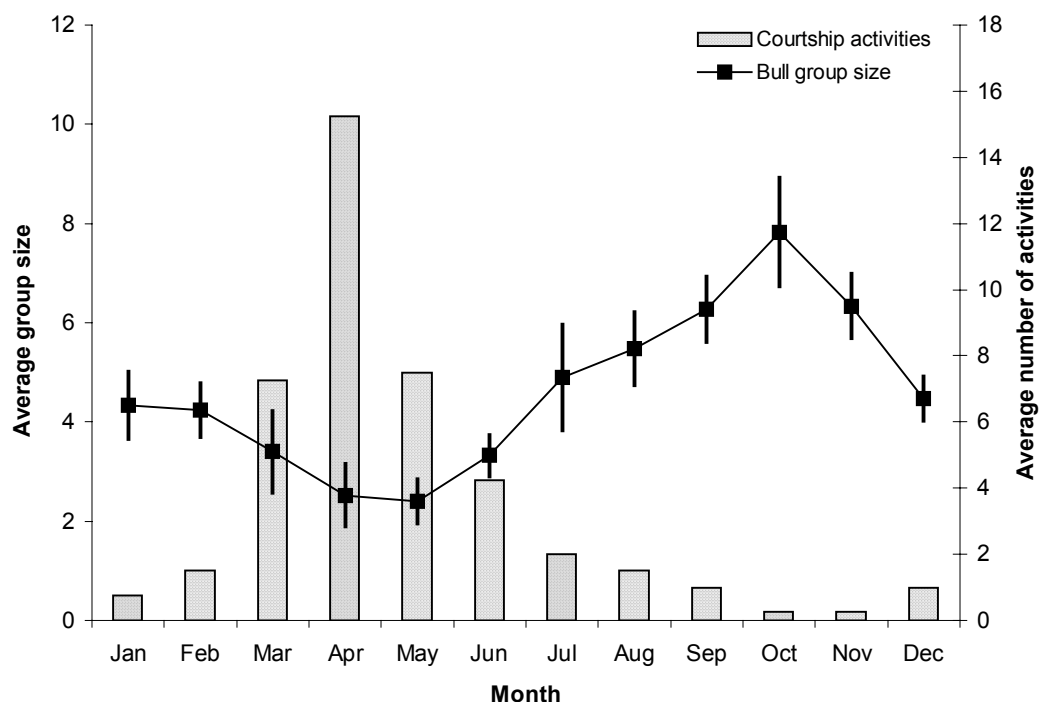


Figure 4. The average proportion of time spent in breeding herds during the breeding (March – June) and non-breeding season by various age classes of radio-collared male buffalo over the study period. Error bars represent the standard error of the mean.

Immature bulls (1 to 4 years) were almost always associated with breeding herds and seldom found in bachelor groups. Young bulls (5 to 7 years) spent a small proportion of their time associating in bachelor groups, but mainly spent their time in breeding herds. This age group did not show any pronounced seasonal pattern to their affiliation with either herd type ($U = 25521.5$, $P = 0.105$, Mann-Whitney U -test). Middle-aged (8 to 10 years) and older bulls (12 years and over) spent the least proportions of their time in breeding herds. For these older age-categories a seasonal pattern was evident where they tended to associate proportionately more in the breeding herds over the breeding season between March and June (Fig. 4)($U = 17044.5$, $P < 0.001$, Mann-Whitney U -test).

Buffalo mortality

Adult bulls were killed more frequently in bachelor groups compared to bulls and cows in breeding herds than would be expected (Table 2). The pattern was highly significant (χ^2 tests, $P < 0.001$) in all four analyses regardless of the mortality or herd type allocation criteria I used. Table 2 presents the results of the analyses using the radio-collar data where the time between herd switches was all allocated as bachelor time. Adult males in bachelor groups experienced an almost five times higher probability of being killed than when in breeding herds (Table 2). Within breeding herds, bulls demonstrated a similar mortality rate (1.35 times) to that of adult cows (Table 2).

Table 2. An analysis of the mortality of adult radio-collared buffalo in differing social environments. The first analysis (A) only included mortalities in which there was data on which herd type buffalo were killed in. The second analysis (B) included all mortalities, assuming the last herd the individual was seen in was the herd type in which they were killed. Expected frequencies were calculated from radio-collar days.

	Bachelor bulls	Herd bulls	Cows	Statistic
A				
Observed	12	1	3	$\chi^2 = 53.33$, df = 2, $P < 0.001$
<i>Expected</i>	<i>2.1</i>	<i>3.4</i>	<i>10.5</i>	
Mortality rate (no. deaths / radio-collar days)	0.001134	0.000059	0.000057	
Relative risk compared to bachelor bulls	1.00	19.08	19.94	
B				
Observed	17	5	12	$\chi^2 = 37.31$, df = 2, $P < 0.001$
<i>Expected</i>	<i>4.7</i>	<i>6.9</i>	<i>22.4</i>	
Mortality rate (no. deaths / radio-collar days)	0.00140	0.00028	0.00021	
Relative risk compared to bachelor bulls	1.00	4.97	6.72	

I used visibility as a surrogate for predation-risk to investigate the reason for the differential mortality of bulls in different herd types. Visibility at mortality sites, was related to herd type and geology (Table 3).

Bachelor groups used habitats with visibility similar to that of habitats where buffalo mortalities occurred (Tukey's HSD test, $P = 0.605$, Fig 5). Breeding herds, however, used significantly more open habitats (high visibility) than occurred at buffalo mortality

sites and habitats frequented by bachelor groups (Tukey's HSD test, $P < 0.001$, Fig 5). Although areas used by buffalo on basalt soils were more open than areas used on granitic soils (Tukey's HSD test, $P = 0.006$), the pattern of breeding herds using more open habitats than bachelor groups and mortality sites was the same for both substrates (Fig 5).

Table 3. Results of a visibility analysis for habitats used by buffalo and mortality sites using two-way ANOVA.

Factors	No. samples	df effect	MS effect	<i>F</i>	<i>P</i>
Herd type	397	2	10.34	33.57	< 0.001
Geology		1	1.74	5.65	0.018
Herd type x geology		2	0.06	0.19	0.832
Error		391			

If buffalo died in habitats similar to that in which they regularly occurred one would expect that adult cows, which associate in breeding herds, would tend to be killed in areas of higher visibility (more open areas) than would bulls. Our data does not support this, however, as at adult buffalo mortality sites, there was no difference with respect to the visibility at sites where males and females died (one-way ANOVA, $F_{(1,55)} = 1.62$, $P = 0.208$).

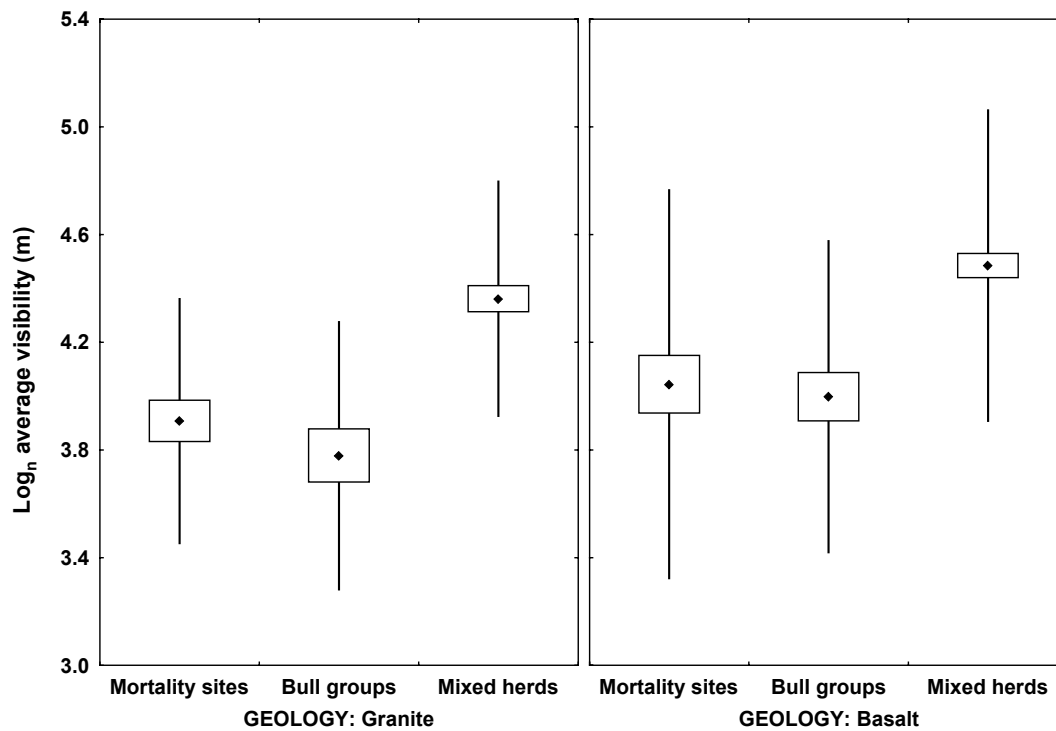


Figure 5. A comparison of the average visibility between habitats utilized by mixed herds and bull groups and sites where buffalo were killed. Open boxes represent the standard error of the mean and the error bars represent the standard deviation.

Discussion

Similar to earlier studies on buffalo (Pienaar, 1969; Sinclair, 1977; Prins & Iason, 1989) our data clearly exhibits higher mortality of adult male buffalo. Lacking empirical data on the context in which bulls were killed, these studies speculated that this skewed sex-specific mortality occurred while bulls were associating in bachelor groups where they likely to be more vulnerable. The dilution effect of associating in a large group (Hamilton, 1971; Bertram, 1978), as well as the fact that lions preferentially select smaller, weaker individuals in the herd (Funston *et al.*, 1998), reduces the relative risk to adult bulls in that social environment. Our data is consistent with these findings, and

based on empirical data from radio-collared animals, demonstrated that in breeding herds there is negligible difference in survival between adult bulls and cows.

Conversely, the probability of survival was substantially less for bulls in bachelor groups compared to bulls in breeding herds, indicating that leaving the breeding herd is undoubtedly an inherently risky strategy for a male buffalo. In elk (*Cervus elaphus*), small group sizes may reduce individual risk of predation through reduced encounter rates by wolves (Hebblewhite & Pletscher, 2002). Similarly, it could be argued that smaller sized bachelor groups may make it more difficult for lions to locate them.

However, I do not feel that this substantially reduces their risk of being located by lions. Buffalo are large ungulates and are not adapted for cryptic predator avoidance strategies. Their characteristic smell is plainly obvious to even our poorly developed human sense of smell, and bachelor groups are generally more sedentary and are usually found close to water (Sinclair, 1977). Consequently they would rank as one of the easier prey species for predators to locate.

Prins and Iason (1989) found that in Manyara the chance of being killed dropped with an increasing distance from cover. In lions, attacks are often more successful at short ambush distances (Van Orsdol, 1984), and increasing grass height and vegetation cover is an important variable in hunting success (Stander & Albon, 1993; Funston *et al.*, 2001). Habitats that have good visibility should therefore be relatively safe, as they provide for early detection and evasion of predators, and may reduce the risk of attack (Cowlshaw, 1997). Our data on buffalo mortality clearly demonstrates that habitats of lower visibility are more dangerous for buffalo. Further, bachelor groups used habitats of equally low visibility as buffalo mortality sites, whereas breeding herds were found

in more open, safer habitats. On this evidence, it is clear that associating in bachelor groups is a substantially more dangerous environment for buffalo bulls.

Consequently, these findings raise the prominent question as to why bulls adopt such risky behaviour. Sinclair (1977) hypothesised that there would be no selection for this behaviour as old, post-reproductive bulls spent the most time in bachelor groups and did not contribute to the survival of their offspring in the herds. He attributed it as an incidental consequence of the functioning of the social hierarchy.

At this point I put forward an alternative hypothesis: primarily middle-aged bulls, but also older bulls represent the core breeders, as a function of dominance (size, strength and condition), and adopt a strategy of moving into bachelor groups to maximise recovery and gain of condition during non-reproductive periods. If this behaviour does elicit a competitive advantage and these animals do indeed obtain mating opportunities, selection would be working in favour of bulls adopting this strategy. Supporting this, in our study both middle aged and very old males demonstrated movement into breeding herds over the breeding season. This is consistent with Funston (1992) who also noted an increase in middle and old aged bulls in the herds during the breeding season.

From our data buffalo bulls exhibit two general types of movement behaviour: (i.) bulls that associate with the herds over the breeding season and move into bachelor groups in the dry season, and (ii.) bulls that associate year round with the breeding herds. This behaviour seems to be largely but not exclusively influenced by age.

From around the age of five years, young bulls (5 – 7 years) show increasing interest in associating in bachelor groups, but spend the majority of their time in the breeding

herds. Although in mature bulls (> 8 years), age may not be a good predictor of dominance (Prins, 1989b), young bulls (< 8 years) do not have the required size and strength to compete with older bulls for dominance and mating opportunities. A prudent strategy for a young bull in this phase of his life would be to maximise his chance of survival while he is growing. The best way to achieve this is in the relative sanctuary of the breeding herds, where the dilution effect of numbers and the active defence by adults in the herd against lion attacks (Schaller, 1972; Mloszewski, 1983; Funston *et al.*, 2001), reduce the risk of predation for a young bull.

Mature males tend to follow a different strategy whereby they spend larger amounts of time in bachelor groups and move into the herds over the breeding season. These individuals are in the reproductively active stage of their life, and their strategy should be aimed at maximising size and strength for dominance encounters to ultimately achieve reproductive opportunities. With the progression of the dry season, and the consequent limited availability of resources, mature bulls spent more time in bachelor groups. Conspecific competition for food is likely to be substantial in large breeding herds usually averaging several hundred individuals, especially as resources dwindle and the size and availability of quality forage is restricted (Prins, 1989a). In addition, the stress of maintaining dominance and competing for oestrus females during the mating season will have taken its toll on the condition of males at this stage in the season. A recent study on buffalo in HiP found that males in breeding herds spent less time feeding, and more time in vigilant or social activities, than bulls in bachelor groups (Turner *et al.*, 2005). This would imply a loss of condition in these individuals, which is consistent with Prins (Prins, 1989b), who documented condition losses of bulls while in

the breeding herds. Jolles (2004) also measured faecal cortisol levels, and found that bulls associating in bachelor groups showed lower cortisol levels than bulls in breeding herds. They attributed these differences to the stress of competition between bulls in the presence of cows while in the breeding herds.

A strategy of associating in a bull group is, however, inherently risky and implies a considerable advantage to adopting this behaviour in order for it to be worthwhile. I propose that spending time in a bull group is a respite from the stress of associating in breeding herds, and that it holds benefit in terms of acquisition of forage over the resource limited part of the year.

In Chapter 3 I investigate the comparative forage quality and movement of bachelor groups and breeding herds, and evaluate the implications for body condition in mature buffalo bulls.

CHAPTER 3

SEASONAL SEXUAL SEGREGATION IN BUFFALO BULLS: IMPLICATIONS FOR BODY CONDITION



Introduction

The highly seasonal nature of subtropical savannas results in variable quality and distribution of forage available for large ungulates (Bell, 1982; Walker, 1993). Nitrogen is arguably the most critical component of forage that limits the performance of grazing animals (Sinclair, 1977; Owen-Smith & Novellie, 1982; Bransby, 1988). As grass plants become mature with the onset of the dry season, crude protein levels decline and invariably become inadequate (Owen-Smith, 1982; Bransby, 1988). In order to satisfy the high energy and protein requirements for reproduction and lactation, animals may synchronise parturition to occur in the growing season when resources are plentiful (Spinage, 1973; Carmichael *et al.*, 1977; Rutberg, 1987). This results in peak periods when the majority of breeding activity occurs. From the perspective of a male, whose ultimate goal is the transfer of his genes to the next generation; it is critical to adopt a strategy that will maximise the ability to out compete challengers for access to females.

In Chapter 2, I demonstrated that buffalo bulls associate in two social environments, namely breeding herds and bachelor groups. Although individuals move freely between these herd types, and may spend varying amounts of time in each, two predominant strategies emerge: (i.) herd bulls that remain with the breeding herd throughout the year, and (ii.) ‘bachelor’ bulls that spend significant portions of their time outside of the breeding herds in bachelor groups, most especially over the dry season.

In KNP, where buffalo have a distinct breeding season (Pienaar, 1969), it is unlikely that a strategy of remaining in the breeding herd year round will translate into much

advantage for access to additional reproductive opportunities. The most obvious benefit for a bull to associate in a breeding herd is the reduced risk of predation afforded by the dilution effect of numbers and cooperative defence (Chapter 2).

In this Chapter, I put forward the hypothesis that a strategy of associating in a bull group over the dry season when resources are limited, has a distinct benefit for buffalo bulls in terms of condition gain. I compare the two strategies and examine the consequences of each.

Methods

Faecal nitrogen

We collected faecal samples from buffalo herds between 2001 and 2003 to investigate levels of faecal nitrogen (N_f). In a concomitant study on our buffalo herds there was a strong relationship between N_f and %N in vegetation utilized by buffalo (Ryan, 2006) and I felt confident to use N_f as a reliable surrogate for the protein content of ingested forage. This alleviates concerns raised by Leite and Struth (1990) about the validity of faecal indicators adequately representing the forage intake of herbivores as the botanical composition changes.

Sampling in 2001 was conducted throughout the KNP in addition to the focal buffalo herds. Ten samples were taken from each herd and the values averaged to obtain a mean value for the herd. For bachelor groups, which frequently contain less than 10 individuals, we only collected samples that were clearly from separate individuals. Only

large faeces were sampled as these were assumed to be from adult buffalo. Samples were collected within 12 hours of deposition to ensure consistent measurement (Leite & Stuth, 1990). In order to conform to veterinary requirements the faecal samples were dried in a convection oven at 65° C for 72 hours. The samples were analysed for nitrogen content at the Institute for Tropical and Sub-Tropical Crops (ITSC), a division of the Agricultural Research Council (ARC) using standard Kjeldahl techniques (AOAC, 1975).

I conducted a three-way ANOVA with herd type, year sampled and season (wet or dry) as the independent variables. Herd type and season were considered fixed effects, and year as a random effect. I classified the dry season as the months between May and October and the wet season between November and April. Secondly, I restricted the data to the dry season and conducted a three-way ANOVA with herd type and substrate (basaltic or granitic soils) as fixed effects and year sampled as a random effect. A comparison of N_f from adult bulls in bachelor groups to random adults in breeding herds (male or female) assumes that there is no difference between sex and age in terms of differential digestive efficiency, which may be expressed as a difference in N_f levels even when foraging on similar material. In order to validate this assumption, I compared N_f levels from animals of known sex and age obtained during large-scale capture operations by a two-way ANOVA, using size category (adult male, adult female and sub-adult) and herd sampled as independent variables. The herd in which the samples were collected was considered a random effect. The results of this analysis indicated that there was insignificant variability of N_f levels between the three age and sex classes (adult male, adult female and sub-adult) within a herd (two-way ANOVA, $F_{(2,12)} = 1.48$,

$P = 0.267$, Table 4, Fig 6). A comparison of randomly collected samples from bachelor groups and breeding herds was therefore acceptable. All analyses were conducted at the 95% significance level ($P < 0.05$) using STATISTICA (Statsoft, 1997).

Table 4. Results of a two-way ANOVA of faecal nitrogen variability within three buffalo size classes, controlling for herd of origin.

Factors	No. samples	df effect	MS effect	<i>F</i>	<i>P</i>
Herd	63	6	0.87	93.07	< 0.001
Size class		2	0.03	1.48	0.267
Herd x size class		12	0.02	1.87	0.068
Error		42			

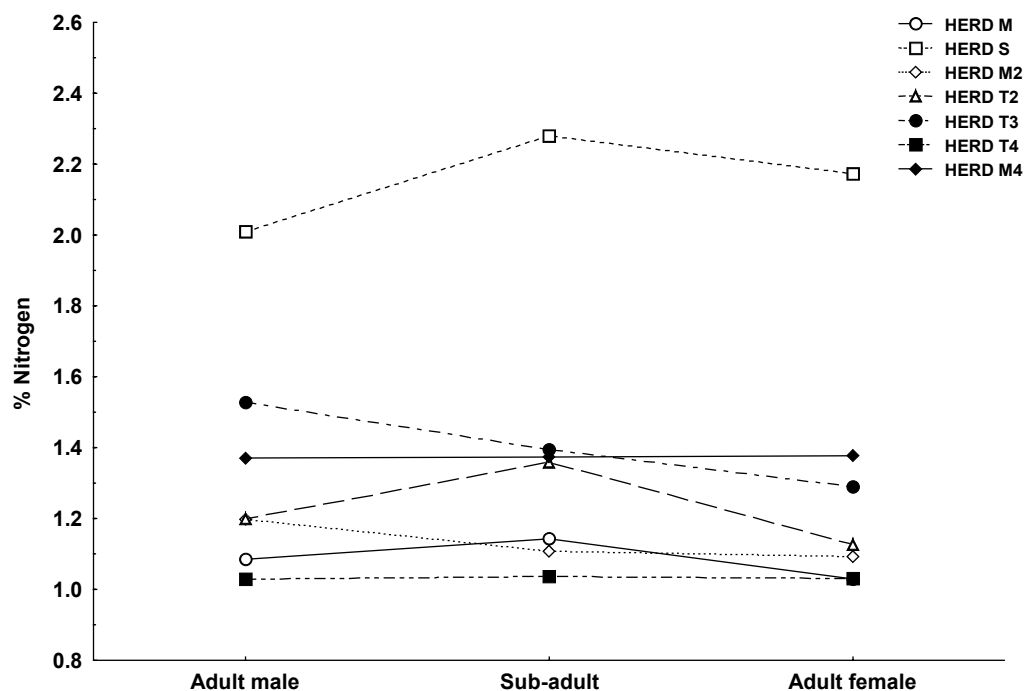


Figure 6. Results of a two-way ANOVA to determine the relationship between faecal nitrogen and buffalo size classes.

Daily movement

We recorded all buffalo groups that were encountered during fieldwork, whether or not they contained radio-collared animals. We also kept a record of the amount of time spent out in the field for each trip, in order to relate buffalo sightings to a measure of effort over the study period.

I used the minimum distance between consecutive sightings to estimate the distance that herds moved on a 24-hour basis. The location of the herds were recorded on a 24-hour interval with a GPS unit, and the shortest distance between the two consecutive sightings was calculated with ArcView 3.2© software (ESRI, 1999). Due to the limited sample size for bachelor groups ($n = 20$), I linked these with the nearest sample from a breeding herd within the same month and on the same geological substrate. Underlying this is the assumption that the pattern of movement for the two herd types is the same, i.e. this assumption would not be valid if one herd type tended to move in a circular pattern and the other in a straight line. I used a two-tailed Wilcoxon's test for matched pairs to determine if the two herd types differed in the daily median shortest distance moved. Whenever herds were located we noted their position in the landscape. I used chi-square analysis to test whether bachelor herds and breeding herds preferentially selected portions of the catenal sequence (crest, midslope, footslope, valley bottom and drainage).

Condition

We gave visual body condition scores to all known buffalo in the field and from video material of the herds between 2001 and 2004. I based our condition index on the same

five-point scale ranging from 1 (very poor) to 5 (excellent), as used in a earlier study on buffalo (Prins, 1989b; Caron *et al.*, 2003), but adapted it by adding half points to increase precision (Caron *et al.*, 2003). This scale is based on a visual assessment of the appearance of the ribs, spine, hips, neck and flank of the animal (Table 5). For the analysis of the data I regrouped the data into a five-point scale by the criteria shown in Table 5, which resulted in an improved normal distribution of the data.

Table 5. Body condition index for buffalo based on Prins (Prins, 1989b), and criteria used to regroup for the analysis to obtain a normal distribution.

Condition	Index	Regrouped index	Description
Very poor	1	1	Shoulder blades, spine and ribs visible
	1.5		
Poor	2	2	Contours of flank and rump concave Ribs visible
	2.5		
Average	3	3	Contours of flank and rump less concave Ribs just visible
	3.5		
Good	4	4	Ribs not visible, flank and rump “filled”
Excellent	4.5	5	Body contours convex Neck thick with fat ridges when bent
	5		

I investigated the change in adult bull's (eight or older) body condition from the late dry season (September to November) to the following breeding season (March to May). I obtained the body condition score for an individual for each year and season by

averaging the observations over that specific period. I determined the herd type that buffalo associated in for each season from our radio-tracking data and visual sightings. Individuals were considered to associate in one of two herd types (bull group or breeding herd) if they spent more than 60% of the time in that social environment for that specific season. Due to the categorical nature of the condition data, I used randomisation tests to investigate the statistical differences in condition gain leading up to the breeding season for bachelor bulls versus herd bulls. For the randomisation test, the average difference in condition gain between bulls in the two herd types was compared to the results of 5000 simulations of the same data where the herd type was randomly re-assigned to individuals. I considered the null hypothesis rejected if less than 5% of the simulations resulted in values greater or less than the actual data. Simulations were conducted in MATLAB 6.1 (MathWorks, 2001).

Results

Faecal nitrogen

The majority of the variability in the N_f data was explained by the effect of year and season (Table 6). During the dry season, bachelor bulls tended to have marginally higher levels of N_f , but this difference only approached significance in 2001 (Tukey's HSD test, $P = 0.079$, Fig 7, Table 6). During the wet season bachelor groups and breeding herds had similar N_f levels except in 2003, when bachelor groups had lower N_f levels (Fig 7). This difference, however, is probably attributable to the fact that all bachelor bull samples for 2003 were taken from basalt substrates, which tended to have

lower N_f levels. When I restricted the data to the dry season and included substrate in a three-way ANOVA (Table 6, Fig 8), mean N_f on granitic soils for bachelor groups tended to be higher than breeding herds although the difference was only significant in 2001 (Tukeys HSD test, $P = 0.005$). On basaltic soils, average N_f for bachelor groups was higher than breeding herds in 2001, but not significantly different (Tukey's HSD test, $P = 0.320$), and similar to breeding herds in the subsequent two years (Fig 8). Thus, bachelor bulls tended to have similar or higher N_f levels than mixed herds during the seasons when nutrients are most limiting.

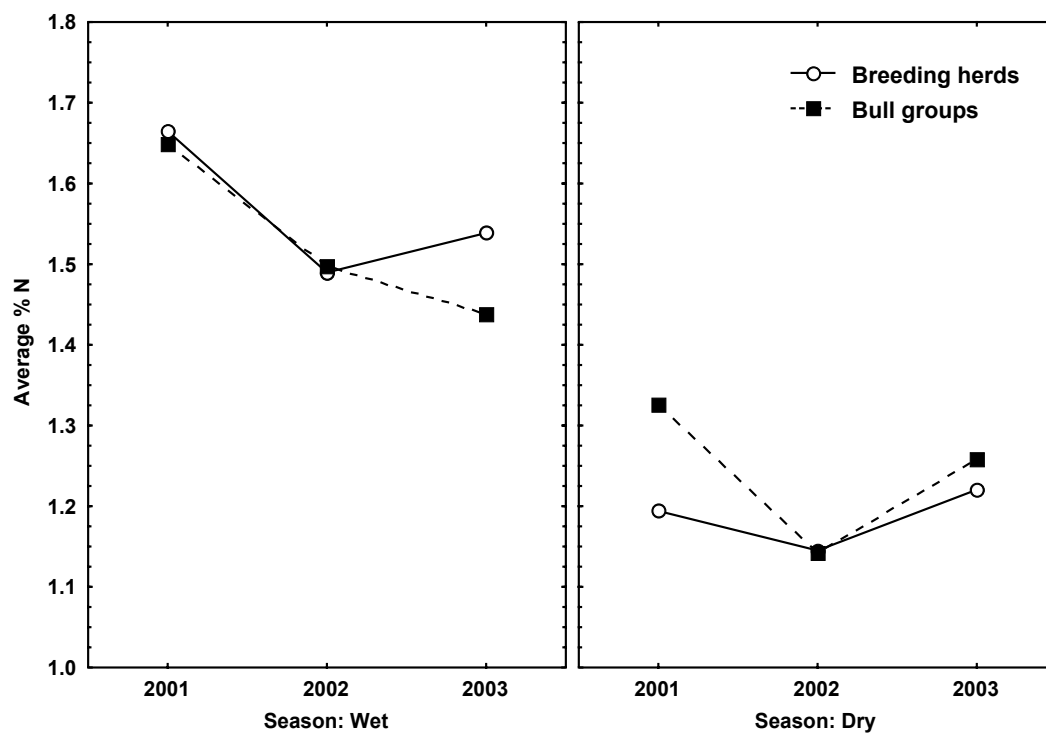


Figure 7. The relationship between season, herd type and average percentage faecal nitrogen for the period between 2001 and 2003.

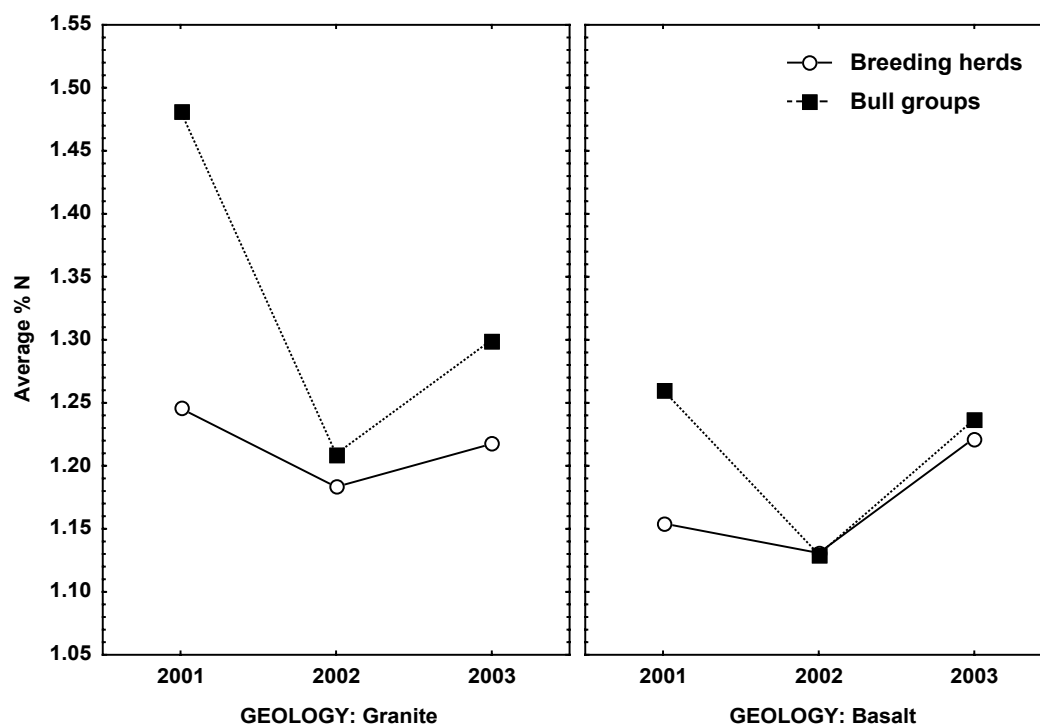


Figure 8. The relationship between geology, herd type and average percentage faecal nitrogen during the dry season for the period between 2001 and 2003.

Table 6. Results of faecal nitrogen analyses using three-way ANOVA on buffalo herds between 2001 and 2003. Interactions marked with an asterisk (*) are significant at the 95% significance level ($P < 0.05$).

Analysis	Factors	No. samples	df effect	MS effect	<i>F</i>	<i>P</i>
Wet and dry season	Herd type	265	1	0.004	0.12	0.765
	Year		2	0.398	18.05	< 0.001*
	Season		1	4.752	60.56	0.016*
	Herd type x year		2	0.033	1.51	0.223
	Herd type x season		1	0.090	2.83	0.235
	Year x season		2	0.078	3.54	0.030*
	Herd type x year x season		2	0.032	1.45	0.237
	Error		253			
Dry season only	Herd type	169	1	0.170	2.54	0.252
	Year		2	0.135	9.40	< 0.001*
	Substrate		1	0.200	4.42	0.170
	Herd type x year		2	0.067	4.66	0.011*
	Herd type x substrate		1	0.040	6.38	0.127
	Year x substrate		2	0.045	3.15	0.046*
	Herd type x year x substrate		2	0.006	0.44	0.647
	Error		157			

Buffalo movement

The median minimum daily movement for bachelor groups was significantly less than breeding herds ($T = 13$, $P < 0.02$, Wilcoxon's test for matched pairs, Fig 9).

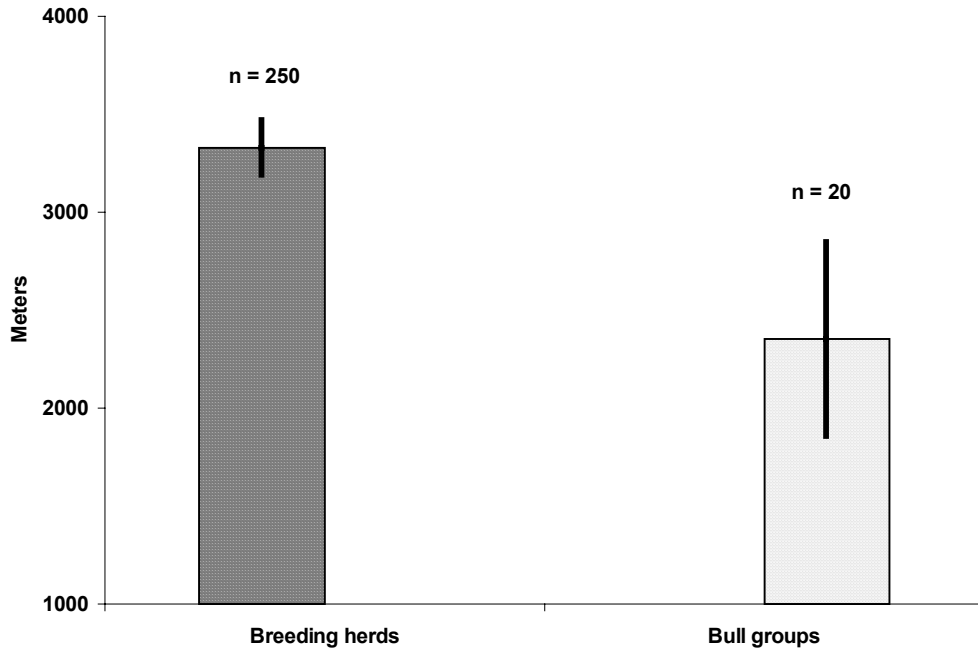


Figure 9. The average shortest distance between 24-hour consecutive sightings of the two types of buffalo herds. Error bars represent standard error of the mean.

The data on the location that buffalo select in the landscape indicates that bachelor groups preferred the bottomlands (valley bottoms and drainage lines), while breeding herds spent relatively more time on the crests ($\chi^2 = 80.38$, $df = 4$, $P < 0.01$; Fig 10).

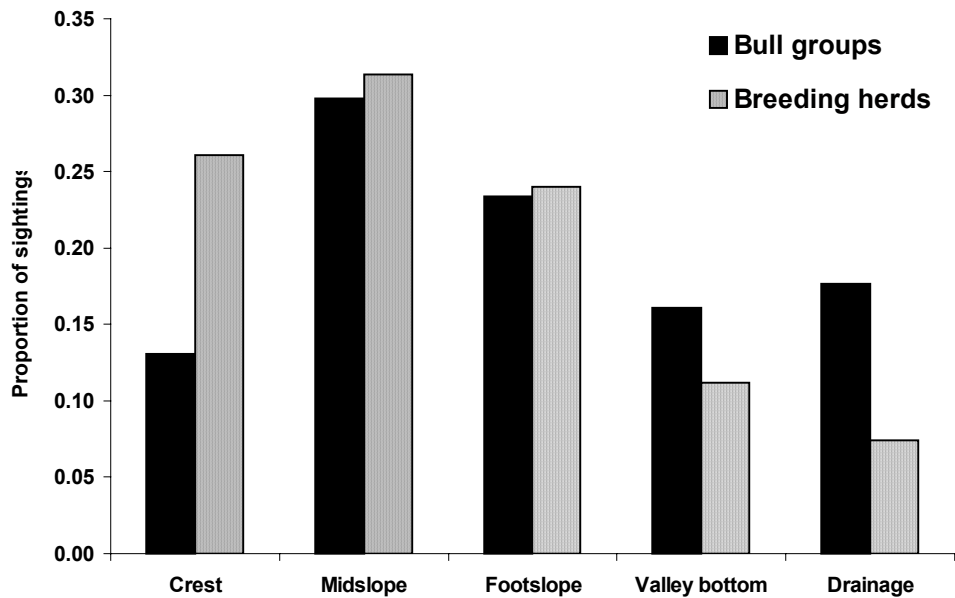


Figure 10. Catena usage of buffalo herds in the KNP. Breeding herds use the crest more often, and valley bottom and drainage line habitats less often than bull groups ($\chi^2 = 80.38$, $df = 4$, $p < 0.01$).

Condition

There was a distinct advantage in terms of condition gain for bulls that spent the larger portion of their time associating in bachelor groups over the late dry season (September to November). These individuals on average gained more condition in the period up to the breeding season (March to May) than bulls that spent their time in breeding herds over the dry season (mean difference 0.54, $P = 0.0043$, Fig 10).

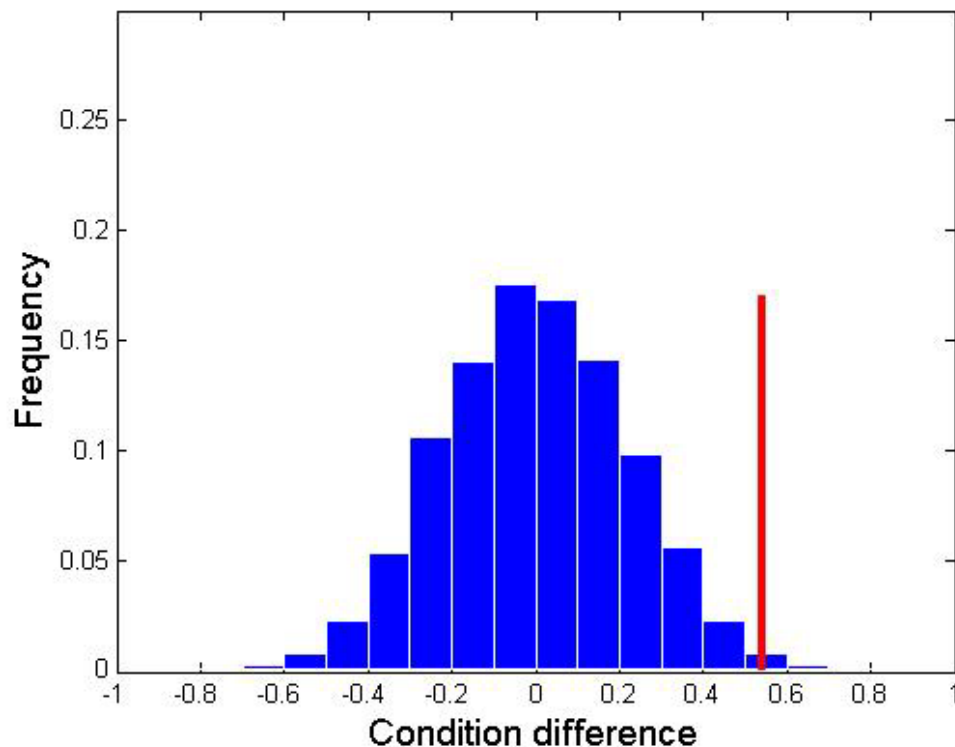


Figure 11. Results of a randomisation analysis on the difference in condition gain between bulls that spent time in bachelor groups in the dry season and bulls in breeding herds. The histogram represents the results of 5000 random reallocations of the herd type to the actual data (red bar), which is significantly different (mean difference 0.54, $P = 0.0043$).

Discussion

Our data clearly points to better living conditions for bachelor bulls. In comparison to bulls in the breeding herds, individuals that spent the majority of the dry season in bachelor groups tended to show a greater improvement in body condition leading up to the breeding season. The physical body condition of an animal is indicative of its fat reserves (Otto *et al.*, 1991; Bruckmaier *et al.*, 1998) and reflects its short-term ability to effectively obtain sustenance from its environment. In subtropical savannas, the late dry

season is the critical period when resources are severely limited as grass becomes senescent and crude protein concentrations decline (Owen-Smith, 1982), and consequently buffalo body condition is at its worst (Caron *et al.*, 2003). As a minimum, the advantage to bachelor bulls appears to be in terms of a net energy saving, as they tend to move shorter daily distances and obtain at least comparable quality forage to individuals in the breeding herds during the dry season.

Although I had limited data on daily movement of bachelor groups, our findings are consistent with Turner (2003) who measured daily movement as a rate, and also found that bachelor groups moved less than breeding herds. Other studies also alluded to the fact that bulls in bachelor groups are more sedentary than their counterparts in breeding herds (Sinclair, 1977; Prins, 1996), and Sinclair (1977) calculated that it could result in an energy saving of 4-7%. In HiP males in bachelor groups spent similar amounts of time feeding as females in breeding herds, whereas males in breeding herds spent the least time feeding. Reproductive activities appeared to be at the expense of foraging time (Turner, 2003). The herd environment is therefore a more physically taxing environment for a bull because of the demands of moving longer distances, competing for resources, and maintaining social status with other bulls in the presence of buffalo cows. An earlier study of Prins (1989b) supports this as he documented condition changes of buffalo bulls as they moved between social environments and found that bulls lost condition while associating in breeding herds and gained condition associating in bachelor groups.

Although differences in N_f between bachelor groups and breeding herds were on the whole not significantly different during the dry season, individuals in bachelor groups were able to obtain forage that is at least of similar quality, and on occasions of superior quality, to that obtained by breeding herds. Bachelor groups clearly preferred the bottomlands (valley bottoms and drainage lines), while breeding herds spent relatively more time on the crests. The bottomlands in the landscape tend to retain moisture that enables plant growth to retain its greenness for longer into the dry season than in upland areas (Macandza *et al.*, 2004). It is likely, therefore, that bachelor groups are able to take advantage of this resource during the dry season due to their smaller group size. The benefit to being part of a smaller group is thus one of reduced competition, and the ability to exploit smaller, potentially superior patches of forage that would probably be quickly depleted within a large herd.

The differences in N_f between bachelor groups and breeding herds seemed to be more pronounced on granitic soils (Fig 8.). According to soil characteristics one would expect granitic soils to retain available soil moisture for longer into the dry season than soils formed from basalt substrates (Scholes & Walker, 1993), which may explain the patterns I observed. Macandza *et al.* (2004), however, working on the same buffalo herds as this study during 2002, found that contrary to expectation there were, no significant differences between basalts and granites with regard to grass greenness retention. They speculated that this could have been due to the fact that 2002 was a very dry year, and that the sodic soils, which are characteristic of granite bottomlands, are heavily utilised, and may have offered inadequate biomass during that period. Our results support this hypothesis as N_f reached the lowest levels during 2002 (Fig 10. &

Fig 11.), and it is likely that in very dry periods that forage quality is uniformly poor over a range of habitats.

Consequently, bulls groups could benefit from spending time during the dry season in the bottomland areas, where they are most likely to find greener grass material, especially on granitic soils. This strongly supports our hypothesis that certain buffalo bulls are able to optimise their energy budget more effectively by being in a bull group during the critical resource-limited time of the year.

In the social environment of a buffalo herd, which may number up to 1000 animals in the KNP (Whyte, 2004), it is unlikely that dominance amongst bulls is maintained in a linear fashion (Sinclair, 1977). In buffalo, dominance and the ability to successfully compete for females is likely to be determined by momentary encounters where aspects of physical condition such as size, strength and fitness are strongly influential to the outcome of the interaction (Prins, 1989b). Males that maximise condition and energy reserves may hold an advantage in terms of physical prowess and reproductive success than males in poorer condition (Clutton-Brock *et al.*, 1982), and may be able to invest in a larger mating effort without compromising their survival (Pelletier *et al.*, 2006). In the KNP where there is a distinct breeding season between March and May (Pienaar, 1969), it is critical for bulls to adopt a strategy whereby they maximise their physical ability to compete during this period to have access to mating opportunities. A strategy of spending time in a bachelor group holds benefits for a buffalo bull in terms of condition gain, and is likely to imply an advantage in attaining this principal goal.

In Chapter 5, I integrate these findings with those of Chapter 2 and then critically evaluate the three main hypotheses that attempt to explain sexual segregation, and how these apply to the KNP buffalo system.

CHAPTER 4

TESTOSTERONE AND CORRELATES OF SOCIAL BEHAVIOUR IN BUFFALO BULLS



Introduction

An understanding of animal behaviour, in particular reproductive behaviour, is critical to our understanding of the functioning of species in an evolutionary framework. In this context, a number of studies have focused on the link between physiological mechanisms and reproductive behaviour, particularly hormone-behaviour responses, which can provide significant insights for the interpretation of sexual behaviour (Ketterson & Nolan, 1992). In many species there is intense competition between males for access to sexually receptive females. Aggressive behaviour and fitness are therefore intimately linked with male reproductive strategy, and are mediated by the existence of, and dynamics of, dominance hierarchies.

A link is apparent where elevated levels of testosterone may facilitate aggressive behaviour (Creel *et al.*, 1997), and social dominance (Pelletier *et al.*, 2003). Testosterone is important in the development of male physical and behavioural characteristics (Lincoln, 1971), and plays a permissive role in the development and expression of sexual behaviour (Lincoln *et al.*, 1972). There is a cost, however, as elevated testosterone levels are associated with reduced survival (Marler & Moore, 1988; Dufty, 1989; Moss *et al.*, 1994) and increased risk of injury (Dufty, 1989), immunosuppression (Folstad *et al.*, 1989; Salvador *et al.*, 1996; Zuk, 1996), and increased energy expenditure (Hogstad, 1987; Ketterson *et al.*, 1991). Males may, therefore, face a cost-benefit trade-off, where elevated testosterone levels are advantageous for mate acquisition and breeding, but detrimental out of the breeding season, resulting in seasonal variation of the hormone (Wingfield *et al.*, 1990).

Here I conduct an exploratory analysis on the relationship between testosterone, social affiliation, and physical characteristics of buffalo bulls. I present evidence on changes in testosterone levels as bulls switch between herd types, and discuss the potential insights this provides to improving our understanding of the social behaviour of buffalo bulls.

Methods

We collected faecal samples from buffalo bulls during 2004 to determine concentrations of faecal testosterone (F_t). Samples were collected opportunistically in the field from known individuals by waiting for buffalo to defecate, or by rectal sampling of individuals whilst immobilized during capture operations. As far as possible samples were kept in a cooler box with ice bricks until they could be frozen for storage at -20°C . In order to satisfy veterinary requirements, samples were oven dried at 60°C for 24 hours to constant weight, and refrozen for storage until they could be transported to the laboratory for analysis.

I conducted all testosterone assays at the Department of Production Animal Studies of the Onderstepoort Faculty of Veterinary Science, University of Pretoria. I used enzyme immunoassay (EIA) techniques to measure testosterone concentrations in the faecal samples (Palme & Möstl, 1994). The reagents for the EIA were from the Institute of Biochemistry, University of Veterinary Medicine and Ludwig Boltzmann Institute of Veterinary Endocrinology (Vienna, Austria).

I also analysed serum testosterone (S_t) concentrations from samples obtained during disease testing capture operations between April 2001 and October 2004. Blood samples were cooled, and the serum was separated from the whole blood by centrifuge as soon as possible, and frozen at -20°C . To conform to veterinary requirements, the sera were inactivated by heating to 56°C for 30 minutes, and refrozen for storage and transport to the laboratory for analysis. I conducted assays on unextracted serum with a solid-phase ^{125}I radioimmunoassay kit (Diagnostic Products Corporation, Los Angeles, CA, USA).

The movements and social affiliation of radio-collared buffalo were monitored as described in Chapter 2. For certain analyses bulls were classified into two groups: (i) “switching bulls” ($n = 6$) that were bulls that spend significant amounts of time in both bachelor groups and breeding herds over the sampling period, and (ii) “herd bulls” ($n = 5$) that spent all or most (more than 70%) of their time in breeding herds. When possible we collected data on body condition score of buffalo bulls (as described in Chapter 3). In addition, during capture operations I took measurements of the testes and neck circumference to the nearest centimetre. Neck circumference measurements were taken just posterior to the head behind the ears, and where the neck joins the body just anterior to the shoulder hump. I averaged these measurements to obtain a neck size index. In the field I also scored beard size of known buffalo bulls in the following size classes: no beard, small beard and large beard.

Consistent with Brown *et al.* (1991), our data showed individuals with high and low testosterone concentrations over the breeding season. Similarly, for analyses on the relationship between testosterone concentrations and buffalo physical characteristics, I classified bulls as High-T or Low-T. High-T bulls had testosterone concentrations in excess of 17 000 ng/g for the faecal data. I only used the faecal data for these analyses, as titres of F_t were significantly correlated with S_t sampled simultaneously in individuals ($r^2 = 0.51$, $n = 39$, $p < 0.001$, Fig 12). In addition, serum hormone levels may reflect momentary measures of short-term variability (Gunarajasingam *et al.*, 1985), whereas faecal measures may reflect a more integrated estimate of secretion and excretion over many hours (Whitten *et al.*, 1998; Creel, 2001), and provide a consistent estimate of daily testosterone levels (Pelletier *et al.*, 2003).

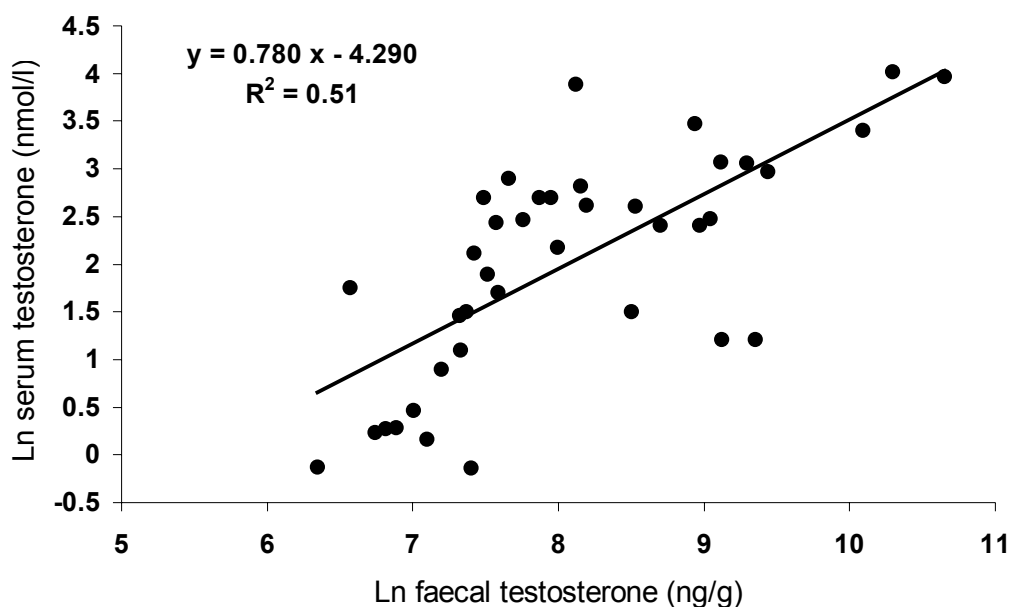


Figure 12. The relationship between serum and faecal testosterone samples obtained simultaneously from the same individual. Data were transformed to the natural logarithm (Ln).

Data were analysed using two-tailed student's *t*-tests or Mann-Whitney *U*-tests when the assumptions of parametric testing could not be met. I analysed relationships in the data with Pearson's Product Moment correlation. Data were normalised by transformation to the natural logarithm when necessary. Data are presented and means and \pm the standard error of the mean.

Results

Seasonal testosterone profile and patterns in differing social environments

A seasonal profile was evident whereby testosterone concentrations were significantly higher during the breeding season than out of the breeding season (F_t : $U = 596.5$, $P < 0.001$; S_t : $U = 1548.5$, $P < 0.001$, Mann-Whitney *U*-tests; Table 7).

Table 7. Seasonal concentrations of serum and faecal testosterone.

		Breeding season	Non breeding season
Serum T (nmol/l)	<i>Mean</i>	14.75	7.11
	<i>n</i>	58	82
	<i>Range</i>	0 - 64.06	0 - 46.49
Faecal T (ng/g)	<i>Mean</i>	12080.6	3508.5
	<i>n</i>	59	35
	<i>Range</i>	568.7 - 91 590	908.4 - 16 434

Bulls classified as “herd bulls” that spent the majority of their time in breeding herds, showed significantly lower concentrations of F_t (2585 ± 293.1 ng/g) over the sampling period than “switching bulls”, who spent larger proportions of time in bachelor groups ($14\,465 \pm 4848.5$ ng/g; $U = 79.5$, $P = 0.034$, Mann-Whitney U -test), but moved into breeding herds for limited periods. Moreover, “herd bulls” demonstrated significantly lower variability of F_t than that of “switching bulls” over the year (F-test, $F = 390.94$, $P < 0.001$). “Switching bulls” had highest F_t concentrations when they were associating in or up to two weeks prior into the breeding herds ($U = 0.0$, $P < 0.001$, Mann-Whitney U -test). The data from the repeat F_t samples and herd affiliation is displayed in Figure 13.

Age and morphological correlates

During the breeding season there was a significant positive correlation between the age of buffalo and the titre of F_t ($r^2 = 0.51$, $n = 55$, $P < 0.001$). Restricting the data to the breeding season, when buffalo demonstrate highest F_t levels (Table 7), it is evident that individuals began to show elevated testosterone concentrations from approximately the age of eight years old (Fig 14). There was no clear pattern to the testosterone concentrations in individuals that were in bachelor groups over the breeding season compared to bulls that were in the breeding herds (Fig 14). The S_t data may allude to a pattern where bachelor bulls show lower testosterone concentrations than bulls in the breeding herds (Fig 14B). The sample size of bachelors, however, was only two individuals, from which it is difficult to make any confident inferences. The pattern is less clear in the F_t data (Fig 14A) where four individuals that associated in bachelor groups showed elevated F_t concentrations. This cross-sectional view of the data however may be misleading, as it is likely that testosterone concentrations may rise in individuals in bachelor groups prior to them moving into a breeding herd. As an example, one of the individuals (the 9 year old, Fig 14A) was sampled in a bull group with a high F_t concentration (29 493 ng/g) and subsequently moved into a breeding herd five days later. Of the other three individuals displaying higher F_t concentrations in bachelor groups (Fig 14A) two were randomly sampled animals on which I had no further history, and one lost his collar a month after sampling. I was therefore unable to confirm if they moved in to breeding herds in a similar fashion.

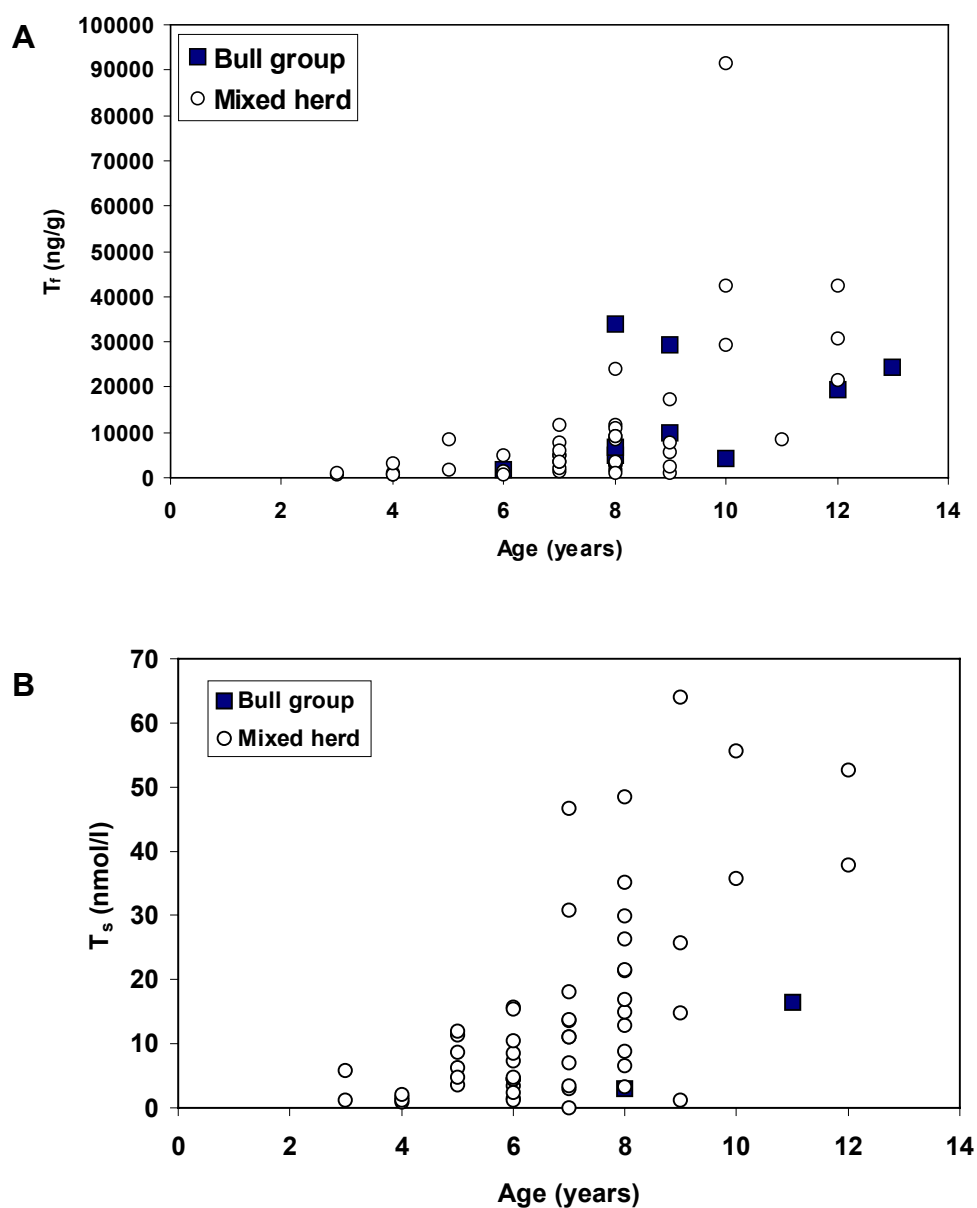


Figure 14. The age profile of faecal (A) and serum (B) testosterone concentrations over the breeding season (March – June).

There were no observable differences in body condition score between High-T (3 ± 0.27) and Low-T bulls (3.4 ± 0.17) during the breeding season ($P = 0.26$).

The mean scrotal circumference of mature bulls over the age of eight was greater in High-T bulls ($46.0 \pm 1.23\text{cm}$) than Low-T bulls ($40.9 \pm 1.16\text{cm}$) ($U = 112$, $P < 0.01$, Mann-Whitney U -test). Additionally, an analysis of mature bulls (8 years +) revealed that High-T bulls had a greater average neck circumference ($133.8 \pm 1.88\text{cm}$) than Low-T bulls ($125.5 \pm 2.18\text{cm}$; $P = 0.05$).

There was a significant effect of beard size on F_t (One-way ANOVA, $F_{(2, 51)} = 8.14$, $P < 0.001$) for bulls over the age of seven years. Bulls with large beards had significantly higher titres of F_t than bulls with small or no beards (Tukey's HSD test, $P < 0.05$). In bulls over the age of seven years, the effect of beard size on age was also significant (One-way ANOVA, $F_{(2, 69)} = 19.75$, $P < 0.001$). Bulls with no beards were on average younger than bulls with small beards, which in turn were younger than bulls with large beards (Tukey's HSD tests, $P < 0.01$). It was therefore difficult to determine if this is an effect of age or testosterone.

Discussion

As with most ungulates, the timing of breeding is strongly influenced by seasonal climatic patterns, specifically rainfall and temperature, to ensure that favourable conditions exist at the time of parturition (Skinner, 1971; Skinner *et al.*, 1973; Gosling, 1986). The seasonal influence on reproductive function has been studied previously in African buffalo (Brown *et al.*, 1991). Consistent with their study, our work demonstrated a clear seasonal testosterone profile with significantly elevated levels

occurring over the breeding season. Unique to this study, however, I was able to relate data on the movement of bulls between social groupings and testosterone levels. A pattern emerges whereby bulls that mainly associated in the breeding herds through the year maintained relatively consistent low F_t concentrations. Bulls that spent larger proportions of time in bachelor groups showed elevated and more variable F_t , and reached peak concentrations when moving from bachelor groups into, and associating with breeding herds.

There is an extensive literature linking aggression and social dominance with elevated levels of testosterone in a broad range of species, including man (Lincoln *et al.*, 1972; Ehrenkranz *et al.*, 1974; Poole *et al.*, 1984; Miller *et al.*, 1987; Chaudhuri & Ginsberg, 1990; Creel *et al.*, 1997; Girolami *et al.*, 1997; Virgin & Sapolsky, 1997; Klukowski & Nelson, 1998; Vleck & Brown, 1999; Chunwang *et al.*, 2004). It is currently accepted that when this correlation occurs, it is unlikely to simply be a case of hormones eliciting the behaviour. Rather, it appears as if the reverse is more probable, where a high frequency of aggressive behaviour stimulates testosterone secretion (Monaghan & Glickman, 1992). It would seem a reasonable assumption that buffalo with elevated F_t are individuals that are high-ranking, or establishing themselves in the upper levels of the social hierarchy (Brown *et al.*, 1991), and may be used as an index of the individual's relative fitness (Pelletier *et al.*, 2003). High-ranking individuals typically dominate breeding opportunities (Clutton-Brock *et al.*, 1982; Owen-Smith, 1993a; Chunwang *et al.*, 2004). Consequently, I would hypothesise the following behavioural model for buffalo bulls: Young or subordinate bulls tend to spend larger amounts of time in breeding herds year round (Chapter 2). These animals have not yet the required

physical ability to compete with individuals at their prime, and consequently can be characterised by low levels of testosterone. Prime bulls, which tend to be older (~ 9 to 12 years), spend larger amounts of time in bachelor groups throughout the year to maximise physical condition, and move into herds over the breeding season for mating opportunities (chapters 2 & 3). These individuals may attain dominance and mate successfully, and demonstrate higher levels of testosterone.

There appeared to be no difference in condition between High- and Low-T bulls. The breeding season, when testosterone levels are elevated is, however, the time of the year when most individuals are able to benefit from abundant forage and condition is at its peak. A confounding factor may be that in the herds, High-T (presumably dominant) individuals are more likely to be engaged in activities relating to courtship and spend less time feeding (Jolles, 2004), which would result in a loss of condition relative to other bulls. Although not significant, the data may allude to this by the fact that over the breeding season the average condition score was higher for Low-T bulls.

A positive relationship between testosterone levels and scrotal circumference has been described in buffalo (Brown *et al.*, 1991), which our data supported. When in peak condition, buffalo bulls tend to gain bulk around the neck and shoulders. In the field I was able to observe this on at least two occasions when bulls that were radio-collared showed a substantial loss in condition due to illness or injury. The previously close fitting radio-collars on these individuals hung visibly loose as their condition worsened. Neck size may, therefore, be a good predictor of physical ability, and our data

demonstrates that in mature animals, High-T bulls indeed have larger neck circumferences.

The beard or dewlap of buffalo may create the impression of a more imposing head and neck during lateral displays to warn-off potential competitors in dominance interactions (Sinclair, 1977; Prins, 1989b). There appeared to be a positive relationship between increasing beard size and testosterone. Although testosterone is necessary for the development of secondary sexual characteristics (Lincoln, 1971; Sapolsky, 1993; Zuk, 1996), it is more likely that in buffalo, beard size is a covariate of age as I found a similar positive relationship between age and beard size.

In short, it seems likely that age is the most important aspect mediating the expression of elevated testosterone levels. Similarly, Pelletier *et al.* (2003) also found a significant relationship between testosterone concentrations and age in bighorn sheep (*Ovis canadensis*). As bulls age they tend to spend larger amounts of time in bachelor groups (Chapter 2). It is therefore difficult to separate the effect of age and testosterone between “switching bulls” and “herd bulls”. Male buffalo maintain growth and weight gained even during old age (Pienaar, 1969). As long as an individual remains in good health it would appear therefore, within limits, that age would provide an advantage in terms of size and strength, and that older bulls would be dominant as has been found in other species (Owen-Smith, 1993a; Pelletier *et al.*, 2003).

Constrained by opportunistic sampling as a result of the difficulty of obtaining faecal samples from free-living buffalo in an extensive study area, our data provides some

insight into the relationship between hormone levels and aspects of social behaviour in buffalo. In light of the fact that much of the data was from this portion of the study was from only one breeding season, a broad interpretation of the results should be made with caution.

Future research should strive to integrate empirical data on social status and reproductive success with endocrine responses and social affiliation of males, and may further unravel the social behaviour of polygynous ungulate species such as African buffalo.

CHAPTER 5

THE ECOLOGY OF AFRICAN BUFFALO BULLS: A SYNTHESIS OF SEXUAL SEGREGATION



It is clear from all previous studies that buffalo bulls demonstrate segregation from females outside of the breeding season for large parts of the year (Grimsdell, 1969; Sinclair, 1977; Mloszewski, 1983; Prins, 1989b; Funston, 1992; Halley & Mari, 2004; Turner *et al.*, 2005). Two hypotheses to explain this have emerged as most promising: the activity budget hypothesis, and the predation-risk hypothesis. Key predictions for the predation-risk hypothesis are that: i) females promote the survival and security of their offspring by the selection of relatively predator safe habitats, with adequate, but not always optimum quality or quantity of food, and ii) males will optimise energy reserves and growth by exploiting areas with abundant high quality forage, or at least modify behaviour to avoid areas where foraging is less productive (Main *et al.*, 1996). This hypothesis is based on the optimisation of behavioural and ecological criteria to improve reproductive success from the perspective of each sex: in males to achieve mating opportunities, and in females to successfully rear their offspring.

In buffalo, our study clearly provides support for this hypothesis. Using empirical data on radio-collared animals over a five-year period, I have demonstrated that adult bulls suffer significantly higher rates of predation than females. This is consistent with other studies on buffalo that have used indirect measures of mortality (see Pienaar, 1969; Prins & Iason, 1989). Furthermore, for the first time in buffalo, I have demonstrated that the risk to adult males occurs specifically while they are associating in bachelor groups and that these groups tend to use inherently risky habitats, whereas females in the breeding herds use safer, more open areas (Chapter 2).

Consequently, there must be some intrinsic advantage in order for bulls to adopt such behaviour. In this study I have shown that under certain circumstances bachelor groups are able to obtain higher quality forage, but even under conditions when forage quality is uniform, bulls adopt a strategy in which they forage optimally to assimilate maximal net energy gain (Chapter 3). Bachelor groups are more sedentary than breeding herds, which could result in energy savings between 4 – 7% (Sinclair, 1977), and the small numbers of individuals enable exploitation of smaller patches of vegetation on which large numbers of animals would rapidly deplete and be forced to move on. In addition, males with larger body sizes hold an advantage in terms of efficiency of digestion and may be able to subsist more effectively by expanding their diet to include lower quality forage when necessary (Demment & Van Soest, 1985). This strategy points to better living conditions for males in bachelor groups, especially over resource-limited periods of the year. Concomitant with this, our data indicated greater returns in terms of condition gain for bulls that spent the dry season in bachelor groups as apposed to remaining in breeding herds (Chapter 3).

In Manyara, East Africa, Prins (1996) although not specifically testing the predation-risk hypothesis, also provided strong evidence to support it in buffalo. Adult bulls clearly ran a higher risk of predation than adult cows (12.9% p.a. vs. 4.4% p.a.) (Prins & Iason, 1989), and living conditions for bulls associating in bachelor groups appeared to be beneficial as bulls gained condition in that social setting, and lost condition in breeding herds (Prins, 1989b).

The activity budget hypothesis is based on sexual differences in activity budgets and movement rates. It assumes that sex related differences in adult body sizes result in differing energetic requirements, which in turn leads to differing foraging patterns (Ruckstuhl & Neuhaus, 2000). Substantial discrepancies in the allocation of time to activities related to foraging, resting and movement will result in separation into groups of similar sized animals, because the costs of synchronisation are too great (Ruckstuhl, 1998; Ruckstuhl & Neuhaus, 2000).

In HiP, Turner *et al.* (2005) did not find evidence to support the activity budget hypothesis. They hypothesised that due to the substantial sexual dimorphism shown in buffalo, that metabolic requirements would force males to segregate because of asynchrony of active and feeding times. Their data, however, revealed that even amongst females there was limited synchrony of grazing times without compromising the ability to maintain cohesive herds. Activity synchrony would, therefore, have little consequence for males to remain associated with the herds.

I contest rather, that their study on buffalo may also allude to evidence in support of the predation-risk hypothesis. Turner *et al.* (Turner *et al.*, 2005) concluded that the high time and energy costs associated with reproduction incurred to bulls while in the breeding herds resulted in segregation, which implies a loss in condition. In their study, individuals in bachelor groups achieved increased grazing and moved less compared to individuals in breeding herds, which is likely to enable recovery and improvement of condition. Implicit to this is seemingly favourable conditions for foraging and growth in

bachelor groups. Furthermore, in HiP where buffalo also coexist with lions, sex ratio's may be skewed in favour of females up to the tune of 1.5:1 (Turner *et al.*, 2005).

In the first study to use a large number of radio-collared bulls, Halley and Mari (2004) in Chobe, Botswana, speculated support for the activity budget hypothesis in the early dry season. Other factors, however, such as dwindling food supplies and predator avoidance appeared to have an overriding effect and forced the bulls into the herds in the late dry season.

The general pattern of segregation appears consistent in buffalo, however, some differences between populations in the duration of segregation over the breeding season have recently become apparent (Turner, 2003). Geographically separated populations may show differing patterns of alternating segregation over the breeding season: bulls move between herd types on a daily (Turner, 2003), or weekly basis (Prins, 1989b); or bulls remain with the breeding herds for months or the entire breeding season (Sinclair, 1977; Halley & Mari, 2004).

Turner (2003) suggested that the behaviour of bulls over the breeding season may depend on the spatial and temporal distribution of oestrous females and the ease with which bulls would be able to rejoin the herd if they left temporarily. Consequently, in populations that are characterized by large herds with many oestrous females and large home ranges, it may be more beneficial for bulls to stay with the herds as they would have regular access to receptive females and would avoid the cost of relocating the herd in a large area. In contrast, populations with small herd sizes and smaller home ranges, may justify a strategy of alternating segregation during the breeding season, where

herds are easy to relocate and bulls can move in and out to keep a check on the availability oestrous females. I updated a version of the table from Turner (2003) which can be found in Table 8. Our study supports this hypothesis as bulls tended to spend long periods in the breeding herds over the breeding season, and areas preferred by bachelor groups were distinct from areas frequented by the breeding herds (Cross, *unpubl data*).

In conclusion, although hypotheses on sexual segregation represent approaches that may not be mutually exclusive, it appears as if the predation-risk hypothesis may be central to explaining sexual segregation in buffalo. Evidence supporting this from two very different ecosystems in South and East Africa suggests that segregation in buffalo has evolved to accommodate selective pressures that operate broadly towards the survival of the species in predator rich environments. Opportunities for future studies on free ranging buffalo, where there have been a number of predator-free buffalo generations to remove any habitat use patterns that may have originated through interactions with large predators, may provide further insights into the evolution of this behaviour.

Management implications and future work

In the context of the bTB epizootic currently infecting buffalo in KNP and other conservation areas, sexual segregation may have implications for the transmission of the disease within buffalo and into other species. Adult buffalo bulls show higher bTB prevalence than adult females (Jolles, 2004), and due to the chronic nature of the disease, adult animals are likely to present advanced stages of the disease where

infection of susceptible individuals is more likely (Rodwell *et al.*, 2001; Jolles *et al.*, 2005). Consequently, bulls may be important vectors of the disease between herds, although recently there is also evidence of long distance dispersal of cows and sub-adult animals (Halley *et al.*, 2002). Test and remove control programs designed to reduce the prevalence of bTB (Jolles *et al.*, 2005) or bTB prevalence surveys mostly focus on breeding herds and are conducted in the cooler dry season to minimize stress on the animals. In the KNP this is the period when between 2% and 11% of the total buffalo population are in bachelor groups (Whyte, 2004), and should be an important consideration when designing and implementing monitoring and management programs.

This study has also demonstrated higher mortality in adult male buffalo. Lions are the primary cause of predation in buffalo (Mills, 1995) and the higher prevalence in adult bulls, along with their vulnerability when in bachelor groups, may increase the risk of transmission to lions.

It is clear from this study that animals associating in bachelor groups are not just old or weakened individuals. Prime breeding individuals are likely to be within the ranks of bachelor groups over the non-breeding season. The bachelor phase of a buffalo bull's life forms an integral part of adulthood and is instrumental to achieving the ultimate aim as a bull: successfully passing on genes to the next generation. Individuals that are hindered by sickness, old age or injury invariably are found singly, often along streams or rivers in proximity to water (pers. obs.). In populations where buffalo are hunted this should be kept in mind as hunting usually takes place in the cooler winter months when

most bulls will be in bachelor groups, and hunting from these groups could risk the elimination of prime breeding bulls. To avoid this, the safest time to hunt buffalo males is from bachelor groups during the breeding season, as these are likely to be non-reproductive individuals. However, knowledge of the local conditions and population is important as populations with small group sizes and home ranges may result in alternating segregation over the breeding season, in which case hunting during that time of the year would still put breeding bulls at risk. This is likely to occur in areas where there is low to moderate seasonality and year round availability of adequate food and water.

Future studies on segregation in buffalo should focus on genetic comparisons between populations that display differences in the duration of segregation during the breeding season. Populations that display alternating segregation over the breeding season may permit more males opportunities to breed than in populations where bulls spend the majority of the breeding season in the herds and mating is dominated by a limited number of individuals. This would provide further insights into the interaction of environmentally mediated behaviour responses and the consequences for genetic heterogeneity in geographically separated populations.

Studies on segregation have largely focused on Northern temperate species (Clutton-Brock *et al.*, 1987; Conradt, 1999; Bon *et al.*, 2001; Weckerly *et al.*, 2001; Mooring *et al.*, 2003) with a relative paucity on African ungulate species (du Toit, 1995; Turner *et al.*, 2005). Further understanding of sexual segregation awaits future studies on subtropical ungulate species representing a range of sexual body size dimorphism.

Table 8. A comparison of the buffalo literature on segregation and factors affecting the availability of females during the breeding season. Adapted from Turner (2003).

Location	Home range (mean annual - km ²)	Breeding season (months)	Herd size (mean)	Typical time spent in herd by ♂'s during the breeding season.
Ruwenzori Park ¹	10	-	130	Months
Hluhluwe iMfolozi Park ^{2, 3}	50	6	100	Days
Lake Manyara ⁴	50	8	260	Weeks
Sabie Sand Wildtuin ⁵	120	4	248	Months
Klaserie ^{6, 7, 8}	204	6	203	Months
Serengeti ⁹	238	5	350	Months
Kruger National Park ^{10, 11, 12}	256	4	245	Months
Chobe ^{13, 14, 15}	-	5	670	Months

Source:

¹ Grimsdell (1969) in Grimsdell and Field (1976); ² Jolles (2004); ³ Turner (2003); ⁴ Prins (1996); ⁵ Funston (1992); ⁶ Ryan *et al.* (*In press*); ⁷ Knechtel, *pers com*; ⁸ Ryan.(2006); ⁹ Sinclair (1977); ¹⁰ Cross, *unpubl. data*; ¹¹ Hay, *unpubl. data*; ¹² Whyte (2004); ¹³ Taolo (2003); ¹⁴ Halley and Mari (2004); ¹⁵ Carmichael *et al.*(1977).

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